

# THE PENAEIDEA OF LOUISIANA

WITH A DISCUSSION  
OF THEIR WORLD RELATIONSHIPS

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By MARTIN D. BURKENROAD

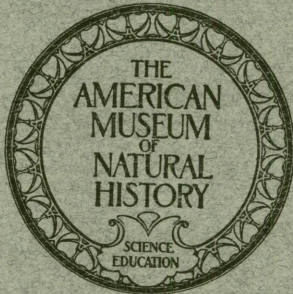
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## Article II.—THE PENAEIDEA OF LOUISIANA

WITH A DISCUSSION OF THEIR WORLD RELATIONSHIPS<sup>1</sup>BY MARTIN D. BURKENROAD<sup>2</sup>

During two years of exploration of the coastal waters of Louisiana, 1929 to 1931, nine species of Penaeidae and six of Sergestidae were captured. Of the Penaeidae, one (*Solenocera vioscai*) has not been previously described, and two others, *Parapenaeus longirostris* (Lucas) and *Trachypeneus similis* (Smith), are additions to the five that have been reported from the region by previous workers. These five species, *Penaeus setiferus* (Linnaeus), *Penaeus brasiliensis* Latreille, *Trachypeneus constrictus* (Stimpson) (which is here replaced by a valid record, since the former one refers to *T. similis*), *Xiphopeneus kroyeri* (Heller), and *Eusicyonia dorsalis* (Kingsley), are represented in the material to be discussed. The ninth species taken is an aristaeine mysis, probably *Gennadas elegans* (Smith) which occurred in the open gulf outside of the strictly littoral zone.

Of the six Sergestidae, only two (*Acetes carolinae* Hansen and *Lucifer faxoni* Borradaile) were found within the littoral area. Preadults of four species of *Sergestes*—a female of *S. atlanticus* H. Milne-Edwards and several specimens in early mastigopus stages which appear to pertain to *S. corniculum* Kröyer, *S. crassus* Hansen, and *S. pectinatus* Sund—were taken in the more oceanic waters forty miles offshore. Another sergestid, *Sergestes arcticus* Kröyer, has been previously noted from Louisiana. I have not taken this species and believe it possible that the determination is erroneous.

## ACKNOWLEDGMENTS

In the course of this work I have been obligated to a number of people, to whom I express my indebtedness. To Mr. Paul Percy Viosca, Jr., under whose guidance I began the field study, and upon whose knowledge of the natural history of *Penaeus* I have drawn extensively, I wish to offer my gratitude for sympathetic counsel as well as for assistance in prosecuting the field study and for many loans of valuable material. Much of the field study was conducted under the auspices of the Louisiana Department of Conservation, to which institution I wish to acknowledge my great obligation, as well as to the Zoölogy Department of the Tulane University of Louisiana; the Louisiana State Uni-

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versity Field Laboratory; the United States Bureau of Fisheries; the Peabody Museum of Natural History and the Bingham Oceanographic Foundation at Yale; the Museum of Comparative Zoölogy at Harvard; and the Museum of the Philadelphia Academy of Natural Sciences; to coöperating individuals, and especially to Mr. Alfred D. Danziger. To Dr. Waldo L. Schmitt I am grateful for the privilege of laboratory and library facilities for four months at the United States National Museum and for permission to examine certain material of *Solenocera*, *Parapenaeus*, *Trachypeneus*, and *Eusicyonia*. To the authorities of The American Museum of Natural History, and especially to Dr. Roy W. Miner and Dr. Willard G. Van Name, I wish to express my deep appreciation of laboratory and library facilities and access to the collections, which have made possible the completion of this work. I particularly thank Mrs. Julia E. Langsam of the same institution for skillful preparation of the typescript.

The collection of Louisiana peneids upon which this paper is based has been incorporated in the collection of The American Museum of Natural History.

#### DESCRIPTION OF TERRITORY EXPLORED

The present investigation has been largely confined to the eastern portion of Louisiana, west to Timbalier Bay, which centers about the present and recently active mouths of the Mississippi River. Within this region use was made of otter trawl, dredge, seine, cast net, dip net, and tow net at all seasons and throughout the diurnal cycle, in both surface and bottom strata, from a hundred miles inland from the coast proper of the Gulf of Mexico to forty miles offshore. The area observed may be roughly divided into three environments, each possessing a fauna distinct in many features from that of the others.

1. ESTUARINE OR "INSIDE" AREA.—The recent Delta interior to the Gulf coast proper, extending north to the level of the north shore of Lake Pontchartrain, comprising an enormous system of sounds, lakes, bays, and bayous, landlocked, but possessing sea connections of varying remoteness. Chandeleur and Breton Sounds, because of their openness to the Gulf, are placed in the next division. The waters of the "inside" area range from fairly salt to fresh with variation in the factors of season, precipitation, wind (which here partially replaces other factors as a cause of tidal movements), accessibility to land drainage (in which river heights and the condition of the levees play an important part), and accessibility to the Gulf, being on the whole much less dense than the "outside" waters. The modal depth is about ten feet, permitting great and sudden variations in temperature. Bottoms are of mud and of detritus principally derived from the marshes, with occasional sandy and weedy patches or reefs of dead or living *Ostrea* and *Rangia* shells. The water is often murky



with unprecipitated silt and is rich in organic débris. Peneïds found in this area are immature *P. setiferus* and *P. brásiliensis*, with a few other forms occasionally occurring in the outer tidal channels.

2. INNER LITTORAL OR "GREEN WATER" AREA.—The littoral waters extending from the open Gulf shore to a variable distance, about ten to twenty miles, offshore. The surface stratum is sometimes completely fresh and silt-laden, especially off the river passes, but the water may be described as generally salt, though of less than oceanic density. The bottom is variable, consisting of mud, shell, or sand, with small quantities of coral and coquina, or sandstone in some localities. Depths range from zero to about sixteen fathoms. There is usually less suspended matter than in "inside" waters. There is a dearth of large algae; the most characteristic bottom cover consists of a hydroid, *Bougainvillea*, and the bryozoan *Bowerbankia*. All the species to be discussed were taken in this area.

3. OUTER LITTORAL OR "BLUE WATER" AREA.—The shallow water of more oceanic type, beyond the "green water." On the few occasions when penetration of this area was feasible, I have noted, at a variable distance offshore, a current-rip extending east and west that separates green water on the north side from the transparent blue water on the south. This rip seems to mark the inner boundary of a current setting strongly to the west. The faunas of the "green water" and "blue water" are quite different in character, while that of the latter, although somewhat similar in general nature, is not identical in nektonic and holoplanktonic (or in meroplanktonic) composition with that of littoral "blue water" of the Gulf Stream as observed at Tortugas, Florida. The bottom consists of fine mud, with some strips of shell reef and patches of sand. The sea plain slopes only very gradually, so that forty miles offshore the usual depth is no more than a few hundred feet. It is probable that all the peneïds found in the inner littoral occur in the outer littoral during a part, at least, of their history; and several species not taken in the inner littoral, and therefore not considered to be strictly a part of the Louisiana fauna, occur there. Further investigation of the outer littoral will doubtless reveal many of the widely ranging semiabyssal and pelagic peneïds.

## SYSTEMATIC ACCOUNT

### **PENAEIDAE** Bate

#### **Solenocerinae** Wood-Mason and Alcock

Solenocerina WOOD-MASON AND ALCOCK, 1891

Parapenaeinae (part) ORTMANN, 1901.

Peneinae (part) ALCOCK, 1901.

Penaeinae, series Haliporae, BOUVIER, 1908.

An examination of the distribution of adult characters among Penaeidae and a study of the larval history of these characters plainly indicate that the three subfamilies customarily established are not completely homogeneous and self-contained and are composed of limited supergeneric groups, the resemblances of which to other subfamilies are often in many characters almost great enough to outweigh their affinities to other members of their own subfamily. At the same time, the larval

histories indicate that the Aristaeinae, together with the members of Wood-Mason's Solenocerina (considered as Penaeinae by later workers), which diverge to some extent only near the end of their development, form a single section of the family. The Penaeinae and Eusicyoninae display a similar resemblance to one another in larval history, which is quite distinct from that of the two former groups. Since the Solenocerinae differ from both Aristaeinae and Penaeinae by a combination of characters found in neither, with the addition of others peculiar to the Solenocerinae alone, and since this combination of characters has about the same importance as that considered sufficient to distinguish the accepted subfamily Eusicyoninae, I feel that it is for the present convenient to revive the subfamily status proposed by Wood-Mason and Alcock. Further study may indicate the advisability of combining the Solenocerinae with the Aristaeinae, and the Eusicyoninae with the Penaeinae.

The Solenocerinae comprise the two genera *Haliporus* and *Solenocera*: the former is characterized by its filiform antennular flagella, the latter by its flattened flagella apposable to form a respiratory tube. The subfamily resembles the Aristaeinae in larval development, accepting, after Gurney, 1924, Monticelli and LoBianco's identification of larva with adult; and differs from Penaeinae and Eusicyoninae in the precocious appearance of the branchial elements and pleopod endopods, and the protracted maintenance of the widely forked telson and unspined pereionic sternites characteristic of earlier larval stages of all Penaeidae. The adults resemble most Aristaeinae and are distinguished from adult Penaeinae by the presence of a cervical sulcus extending nearly or quite to the dorsum of the carapace (as in early larvae of Penaeinae); a distinct tubercle on the ocular peduncle (as in some Penaeinae); epipodites on all coxae from VIII to XIV; a functional, filamentose anterior arthrobranch on XIII (as in reduced form in the penaeine *Artemesia*); the occasional presence of podobranchs behind VIII; and the weak furcation of the epipodites (as in a few Penaeinae). The adults resemble Penaeinae and are distinguished from Aristaeinae by the presence of a scale at the external angle of the ocular somite (which is, however, indicated as a faint elevation in some Aristaeinae); the hypertrophy into an elongate scale of the ciliated protuberance which is found in some Aristaeinae and Eusicyoninae on the inner proximal margin of the basal segment of the antennular peduncle; and the presence of a specialized telson, with well-developed terminal point and reduced lateral armature. The adults resemble both Aristaeinae and Penaeinae and differ from Eusicyoninae in the presence, in both males and females, of a



tuft of setae on the proximal margin of the propodus of the first chelipeds, the presence of pleurobranchs behind IX, and of exopodites on the maxillipedes and pereopoda. The adults (except *Haliporus thetis* Faxon) resemble most adult Eusicyoninae and differ from all other Penaeidae in that they lack lateral telson armature other than a subterminal pair of fixed spines, equivalent to the distalmost of the primitive four pairs. The ventral rostral teeth occasionally present in *Haliporus* resemble those of Eusicyoninae and some members of the *Penaeus* series of Penaeinae and probably are derived, as they have clearly been in Eusicyoninae, by enlargement of some of the dorsal teeth into a false tip. The Solenocerinae resemble some of the species of the *Penaeus* series of Penaeinae and differ from other Penaeinae and the Eusicyoninae in the possession of an open thelycum. A peculiar thelycum of simple enclosed type, in which a pair of invaginated spern receptacles open at the posterior margin of the twelfth somite, appears to occur in *Gennadas* of the Aristaeinae, according to figures by Kemp, 1909; but most other Aristaeinae seem to have an open thelycum.

The Solenocerinae are peculiar in their possession of a postorbital spine, which is reported as lacking only in *Solenocera maldivensis* Borradaile.

### **SOLENOCERA** Lucas

#### ***Solenocera vioscai*, new species**

Figures 1 to 4

**MATERIAL.**—Type female, total length about 95 mm.; carapace without rostrum, 21 mm. Paratype female, total 84 mm., carapace 19 mm. Catalogue No. 6698, American Museum of Natural History.

**DISTRIBUTION.**—Two specimens were taken by trawl in the "green water" about five miles off Pass à la Loutre, at a depth of 15 fathoms, in March, 1931. A late mysis larva, presumably of this species, although perhaps attributable to *Haliporus*, was taken in the outer littoral in May. The only report of the genus in the western Atlantic seems to be of three females taken at a depth of 31 fathoms in the Gulf of Paria on the Venezuelan coast, and identified by Smith, 1885, somewhat doubtfully—without direct comparison—with the Mediterranean and eastern Atlantic *S. membranacea* (H. Milne-Edwards). An examination of this Venezuelan material shows it to be identical with that from Louisiana and distinct from *S. membranacea*.

**DESCRIPTION.**—Rostrum approximately to the basal third of the second article of the antennular peduncle in the larger specimen; to the end of the first article in the smaller; horizontal, narrow; armed above with nine teeth becoming regularly smaller and more closely spaced from behind to front. The posterior three teeth are behind the orbital margin in both specimens, but the third is barely so in the larger specimen. The posteriormost tooth is not definitely set apart from the remainder of the series. It is less than a third of the distance between the orbital margin and the upper end of the cervical groove from the latter. Ventral margin ciliated from within

one-seventh of its base almost to the tip, which tapers regularly to an acute point. A ridge slopes up along the lateral surface of the rostrum from the orbital margin to the anterior margin of the penultimate tooth. Postrostral carina high, continuing almost to the posterior margin, interrupted by a deep depression at the level of the cervical groove. Orbital angle sharply dentiform. Slightly above the anteroinferior angle of the carapace is a completely marginal pterygostomial spine, the area posterior to it not displaying a buttress. Hepatic and antennal spines distinct but small. Postorbital spine large, acute, and placed well behind the anterior margin. Cervical groove deep; its accompanying carina ending just beneath and behind the depression in the dorsal keel, slightly closer to the posterodorsal margin of the carapace than to the orbital margin. Carapace more laterally compressed anterior to the cervical groove than posterior to it. The carina posterior to the anterior cervical (subhepatic) sulcus runs straight to the unarmed branchiostegal prominence, beyond it bending somewhat ventrad, and again anteriad, so that the terminal portion of the sulcus, beyond the branchiostegal prominence, is set off as an oval pit.

Pleon much less deep than the cephalothorax; dorsally sharply carinate on segments 6, 5, 4, and the posterior two-thirds of 3; the posterior dorsal margins of 3, 4, and 5 are cleft, while the carina of the 6th segment terminates in a spine. Telson sulcate above to the level of the lateral teeth, a little less than a third of its length from the tip. Terminal portion of the telson with neither sulcus nor keel. The single pair of lateral teeth is short, fixed, small, hardly diverging from the margin of the telson, although it is longer and more divergent in the smaller specimen than in the larger, figured one. There are no mobile lateral spines. Between the bases of each pleopod pair is a median sternal spine, the series growing smaller from front to rear. The anterior two larger spines are bluntly conical with a broad base. The telson does not reach the tip of the endopod of the uropod, and is overtopped by the exopod.

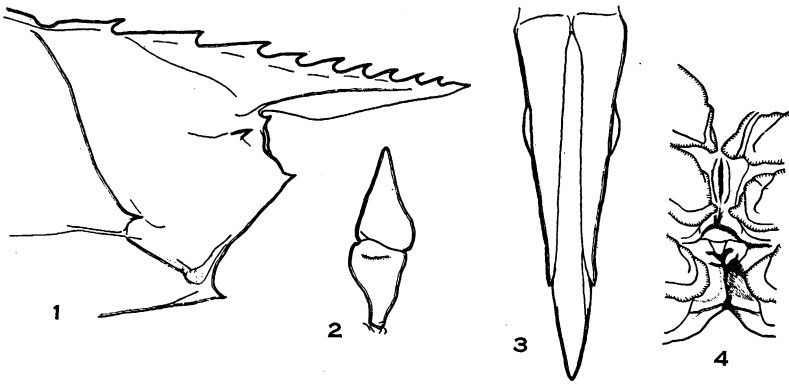
It may be noted that, as probably throughout the genus, the calcification of the tergum of the first pleonic somite is limited to a narrow anterior bridge, a construction that presumably facilitates the reflexing of the body.

A channel leads anteriorly from an atrium enclosed between the mandibular palpi, the antennal peduncles, and the anterior sternites, and communicating with each gill chamber, through a corridor between the antennal scales and the apposed antennular peduncles, to the tube formed by the antennular flagella. The coupling between corridor and tube is effected by strong overarching cilia on the ultimate segments of the antennular peduncles. The lower part of the flagellar tube is formed by the apposition of the median margins of the inferior rami; the upper surface is closed by the superior rami. All these parts are locked together by cilia on their margins. I would suggest that this complex arrangement of diverse organs into a single system has a functional significance, namely, the delivery of clean respiratory water to the gill chambers when the animal is buried in silt, and that probably there will be found in this genus a sedentary habit and a reversal of the direction of waterflow usual among decapods. The modification of the first pleonic tergum noted above, to permit a much reflexed attitude, is perhaps a correlate of the burrowing habit.

The tubercle of the inner distal surface of the ocular peduncle is present but inconspicuous. The antennular peduncle does not quite reach the tip of the antennal scale. The antennular flagella are rather narrow, the inferior about twice as wide as the superior. They taper very slightly to the abrupt tip and are about twice the rostral length longer than the carapace plus the rostrum. The antennal flagella are



not entire but appear to have been very long. They are slender and taper only slightly in the portion present. The distal segment of the mandibular palp is somewhat longer than the proximal, with an expanded base, narrowing to a slender tip, slightly greater than the extreme width of the proximal segment. It may be noted that there appears to be some sexual dimorphism in the mandibular palp of *Solenocera*. The gill bailer of the second maxilla has an even external margin. The endopodite of the third maxilliped exceeds the antennal scale by its dactyl and about half the propodus. The pereiopods are all slender, and possess small slender exopodites of which those of the anterior legs are longest, but on the first leg fall short of the distal end of the ischium, and on the second leg fall far short of it. The basis and ischium of the first leg, and the basis of the second leg, are armed with long slender spines. The third legs are very long, exceeding the antennal scale by one-third of the carpus; this segment is extremely elongate, exceeding the combined length of the segments proximal to it,



Figs. 1-4. *Solenocera vioscai*, new species.

1, carapace, lateral surface, anterior portion, larger cotype female; 2, left mandibular palp, ventral surface; 3, telson, dorsal surface; 4, thelycum.

and is proximally much stouter than distally. The first pleopod, as in the females of many Penaeidae, has a small inner ramus. The branchial formula is that of the genus. As in the Aristaeinae, but as in *Penaeus* and *Heteropenaeus*, and *Funchalia* alone of Penaeinae, there is a pleurobranch on somite XIV and an epipod on IX. As in some Aristaeinae only of Penaeidae, there is an epipod and two functional arthrobranchs on XIII. The rudimentary podobranchs reported in some species of *Haliporus* are absent, and the exopodites of the posterior two pairs of maxillipeds are well developed.

The thelycum consists of a series of prominences and depressions of sternites XIV, XIII, and the posterior part of XII, for the attachment of the glutinous fixation appendages of the pair of large spermatophores [which I have observed in *S. hextii* Wood-Mason, and in *Haliporus robustus* (Smith) although not in the present form]. Among the conspicuous structures of this "holdfast" area are the pair of broad setose spines placed one on either side of the median line on the anterior part of sternite XIV, the posteriorly directed tips of which meet in the median line in the larger specimen. These spines and their buttresses are equivalent to the semilunar ridges in a similar

position in *Penaeus setiferus*, and probably to the lip of the transverse groove of other Penaeinae and Sicyoninae. The sternum behind the spines is not elevated into a knob or tooth. Sternite XIII is posteriorly much elevated, with an emarginate posterior edge equivalent to the posterior part of the median plate of Penaeinae and Sicyoninae. A median longitudinal ridge on XIII represents the anterior portion of the median plate.

Venezuelan specimens in the collection of the U. S. National Museum agree in general with the above but exhibit some differences. In the smallest specimen, the carapace length of which is 11 mm., the rostral spines number only six, and the dorsal carina is not very conspicuous posterior to the cervical groove. The length of the appendages is rather variable in the material examined, the antennular flagella and the third leg being somewhat shorter in the Venezuelan than in the Louisiana specimens. The thelycum of the largest individual, of which the carapace measures 17 mm., is similar to that of the larger Louisiana type. In a smaller specimen the paired spines are conspicuous but unproduced knobs as in the smaller Louisiana individual. In the smallest Venezuela female the thelycum is completely unarmed, and may be regarded as juvenile.

COMPARISON WITH OTHER SPECIES.—Of the fourteen or fifteen described species of *Solenocera* and *Parasolenocera*, four or five (*S. hextii* Wood-Mason and Alcock, *S. melantho* De Man, *S. koelbeli* De Man, *S. pectinata* Bate, and probably *S. lucasii* Rathbun lack both a branchiostegal and a pterygostomial spine.

*S. faxoni* De Man and *S. (Parasolenocera) annectans* Wood-Mason and Alcock have a branchiostegal spine. These two species are certainly very closely related; the former seems distinguishable from the latter chiefly by its lack of a dentiform orbital angle, its much shorter rostrum, and its less tapering antennular flagella. The untruncated antennular flagellum employed by Wood-Mason and Alcock to distinguish *Parasolenocera* from *Solenocera* is evidently not a highly significant character, while the "abdominal hump" is perhaps merely an appearance caused by the reflexing of the pleon, since the third and fourth pleonic somites seem little deeper than in other species. *Parasolenocera* is not entitled to generic rank, such as has been given it by De Man, 1911. A subgeneric use of the name is possible on the basis of the branchiostegal position of the lowermost spine of the carapace; but in this case the distinction of the group of species with pterygostomial spine and of that completely without armature as subgenera of equal rank with *Parasolenocera* would seem proper. Until it has been shown that there is a correlation between several characters indicating that a natural



subdivision exists, I do not believe that a formal separation of the three groups is permissible.

*Parasolenocera maldivensis* Borradaile, 1910, differs from all other Solenocerinae in that the postorbital spine is described as lacking. This species seems to show no resemblance at all to the species for which *Parasolenocera* was established. Neither branchiostegal nor pterygostomial spine is mentioned as present; the antennulae are neither figured nor described; the figure shows no conspicuous abdominal "hump." The figure is widely at variance with the description in showing a pair of lateral telson teeth and two instead of four postrostral teeth. The "trace of a tooth below near the end" of the rostrum is reminiscent of certain species of *Haliporus*. I am unable to fix the affinities of this form to any other species of *Solenocera*, and, should the absence of a postorbital spine be confirmed, propose for its reception the new subgenus **Transolenocera**. It may be noted that the absence of a postorbital spine in the figure of *Haliporus robustus* (Smith) by Milne-Edwards and Bouvier, 1909, is an oversight.

The remaining species of *Solenocera*—*S. vioscai*, *S. agassizii* Faxon, *membranacea* (H. Milne-Edwards), *africanus* Stebbing, *comatus* Stebbing, *novae-zealandiae* Borradaile, and possibly *crassicornis* (H. Milne-Edwards)—have a marginal, pterygostomial spine. Of these species, *S. vioscai* is separable from *S. membranacea*, with which it has been confused, by three important differences in structure:

- 1.—The anterior cervical carina of the latter, at its anteroventral end, turns ventrad at a sharp angle and does not return anteriorad to set off the terminal part of the sulcus as a depressed oval area.

- 2.—The dorsal cervical carina of the latter is interrupted some distance above the hepatic spine by a deep depression.

- 3.—Sternite XIV of the latter is elevated into a blunt median tooth posterior to the depressed area from which spring the paired spines in *S. vioscai*. In *S. membranacea* the depressed area bears a scarcely divided setose knob.

*S. vioscai* differs from *S. membranacea* in other characters as follows:

Its rostrum is longer, more horizontal, and narrower, with a larger modal number of dorsal teeth than that of *S. membranacea*. The posterior tooth of its rostral series is less than a third of the distance between the upper end of the cervical groove and the orbital margin from the former, instead of being about halfway, as figured by Kemp, 1908, for *S. membranacea*. The postrostral carina of its carapace is usually higher and more distinct, and the notch at the level of the cervical groove is deeper than in the European species. The posteroinferior margin of its sixth pleonic segment, just behind the spinule, is concave rather than convex so that the spine is set at the apex of a slight angle of the pleuron. The median spines of its anterior two pleonic sternites are usually blunt and uncurved, whereas in *S. membranacea* they are slender, sharp,

and curved anteriorly. Its telson is shorter, not exceeding even the endopod of the uropod. Its third and fifth legs are usually longer and slenderer than in *S. membranacea*. Its gill bailer has an even external margin, whereas in *S. membranacea*, as figured by Kemp, this margin is considerably expanded in its posterior portion. The dactyl of its second maxilliped is longer than the propodus. The exopodites of its pereonic legs are shorter and slenderer than in *S. membranacea*, in which those of the first leg exceed the distal end of the ischium and those of second almost reach it.

I have compared the five specimens of *S. vioscai* with a male and a female of *S. membranacea* from the Mediterranean in the collection of the U. S. National Museum. The characters listed above, in which *S. vioscae* is compared with Kemp's figures, were not examined in available European material. I am inclined to believe that Kemp's figure may be inaccurate in some or all of these features, as will be discussed below under *S. africanus*. In the unrecurved ventral end of the hepatic groove, the two Mediterranean specimens examined agree with the figures published by Kemp, 1910, and the description by De Man, 1911. In characters of rostrum, telson, postrostral carina, and proportions of appendages, they agree with descriptions by Kemp, 1910, and Bouvier, 1908.

*S. vioscai* is separable from *S. africanus* as figured by Stebbing, 1917a, by the deep cleft in advance of the second rostral tooth from the orbital margin of the latter, which bites as deep as the lateral ridge; by its undentiform orbital angle; by its postorbital spine placed very near the anterior margin; by its pterygostomial spine with a postmarginal buttress; by the spine on the cervical groove dorsad the hepatic spine, like that of *S. hextii* Wood-Mason; and by the quite different cutting edge of the mandible. *S. africanus* is said by Stebbing to lack the terminal spine of the dorsal carina of the sixth pleonic segment, but in *Solenocera* species near *S. africanus* of Calman, 1925, this spine is present.

It may be noted that Stebbing describes *S. africanus* as very close to *S. membranacea*, a relationship not confirmed by the somewhat obscure figure. I observe that a female of *Solenocera* in the collection of The American Museum of Natural History, taken at a depth of 150 fathoms, forty miles northwest of Cape Town, seems to resemble quite closely the Mediterranean and eastern North Atlantic *S. membranacea*, except that its antennular flagella are longer, in agreement with Stebbing's description of *S. africanus*, being three times the rostrum longer than the carapace plus the rostrum. As in *S. vioscai*, but not in Kemp's figure of *S. membranacea*, the external margin of the gill bailer is not expanded, and the epigastric tooth of the carapace is quite close to the cervical notch. As in *S. vioscai* and Kemp's figure, but not in Stebbing's figure, the cutting edge of the mandible bears two distal teeth. As in *S.*

*vioscai* and in *S. africanus* as described by Stebbing, but not in Kemp's figure, the dactyl of the second maxillipeds is longer than the propodus. The third pleonic somite is carinated, as is the terminal portion of the telson. I am inclined to believe that this African specimen is equivalent to the described female of *S. africanus* Stebbing and that the figure of the male of that species is either incorrect or represents a species other than the described female. I am doubtful as to whether other characters of those mentioned than the longer antennular flagella actually distinguish the African specimen from *S. membranacea*. Balss, 1925, has expressed doubt of the distinctness of Stebbing's species. For the present I should regard the South African species of the genus as consisting of a possible varietal form of *S. membranacea*, in part included in Stebbing's *S. africanus*; a possible species of unknown affinities, to which the name *S. africanus* may be restricted, if the figure should prove accurate; *S. comatus* Stebbing, and possibly Calman's *Solenocera* species, which may perhaps be conspecific with Stebbing's male of *S. africanus*.

*S. vioscai* seems clearly distinguishable from its closely related Pacific coast congener, *S. agassizii* Faxon, 1893 and 1895, by its antennular flagella, those of the latter being much shorter and broader and subequal in breadth; by its modally more numerous rostral teeth; by its more distinct postrostral carina, deeply notched above the cervical groove; by the different form of the ventral margin of its orbit, which descends less sharply to the antennal spine; by its less steeply descending anterior cervical sulcus; by its somewhat longer appendages; and by the somewhat different sculpture of its thelycum.

*S. vioscai* seems distinct from *S. comatus*, as figured by Stebbing, 1915, by its mandibular palp, that of the latter having a proximal segment much larger than the ultimate; by its longer antennular flagella; by its longer, shallower rostrum, with more numerous dorsal teeth of which more than two are behind the orbital margin, and with an acute rather than sabre-shaped tip; by its dentiform orbital angle; by its dorsal carina being notched above the cervical sulcus; and by the much smaller lateral spines of its telson.

*S. vioscai* seems also distinct from *S. novae-zealandiae* Borradaile, 1916, which appears to bear a considerable resemblance to *S. comatus*, by the position of what appears to be the hepatic spine of *S. novae-zealandiae* (termed "branchiostegal" in the accompanying text) quite low on the sides of the carapace.

The description of *S. crassicornis* H. Milne-Edwards, 1837 (not

Wood-Mason and Alcock, 1891, which lacks the pterygostomial or branchiostegal spine said to be present in Milne-Edwards' form by Bouvier, 1908), is meager, but this species is evidently distinct from *S. vioscai*, since it has much more numerous rostral spines and lacks a lateral armature on the telson.

The descriptions of *S. distincta* (De Haan, 1850) of Bouvier, 1908, and De Man, 1911 (not of Koelbel, 1884, and Balss, 1914, which lack a pterygostomial spine) are not complete, but this species appears to differ from *S. vioscai* by its shorter rostrum with fewer spines, its shorter fifth legs and third maxillipeds, and in having the carpus of the third legs equal in length to the merus. Material from China and Japan, in the collection of the U. S. National Museum, referred to this species and examined for comparison with *S. vioscai*, lacks a pterygostomial or branchiostegal spine and appears to be referable to three different species: *S. melantho* De Man, *S. koelbeli* De Man, and the *S. crassicornis* (?) of Wood-Mason, 1891 (not of Milne-Edwards, if Bouvier's statement that the branchiostegal spine of this species is present is based on actual material. Through the kindness of Dr. Ch. Gravier of the Paris Museum I have been informed that Milne-Edwards' type is no longer in existence). Balss, 1914, in synonymizing his specimens of *S. koelbeli* with *S. distincta*, apparently overlooks the fact that De Man, 1911, has confirmed the occurrence of a pterygostomial spine in the type of the latter.

### Penaeinae<sup>1</sup>

Carapace without postorbital spine; cervical sulcus not extending to the dorsum. Ocular somite without a greatly produced pair of median projections; with a more or less conspicuous pair of projections from its lateral portions. Telson with well-developed terminal spine. Ocular peduncles with some inconspicuous vestiges of a median tubercle. Proximomedian margin of the antennular peduncle produced as an elongate scale. First chelipeds with setiferous organ in both sexes. No podobranchs behind VIII; no epipodites behind XII, epipodites usually forked; no filamentose anterior arthrobranch on XIII, except in *Artemesia*. Pleopoda posterior to the first pair biramous.

The subfamily, as here defined, differs from that of recent authors by the exclusion of Solenocerinae and from earlier definitions by inclusion of some of the "Parapeneinae." It seems to consist of four series of

<sup>1</sup>For a discussion of certain penaeine genera not considered here in detail, and especially of the three genera heretofore confused under the name *Penaeopsis*, see Burkenroad, 1934, 'Littoral Penaeidea chiefly from the Bingham Oceanographic Collection, with a revision of *Penaeopsis* and descriptions of two new genera and eleven new American species,' Bull. Bingham Ocean. Coll., IV, Art. 7 (in press).

genera. The first of these series contains *Penaeus* Fabricius; the closely related *Heteropenaeus* De Man; and *Funchalia* Johnson, including a new subgenus, *Pelagopenaeus*, heretofore confused with *Penaeus*. The second series is composed of the first (a new genus) and second (*Metapeneus* Wood-Mason and Alcock) of three genera which heretofore have gone undistinguished under the name "*Penaeopsis*"; *Atypopeneus* Alcock; *Parapeneopsis* Alcock; *Xiphopeneus* Smith; and *Trachypeneus* Alcock. The third series is composed of the third genus (*Penaeopsis* Bate) of "*Penaeopsis*"; *Parapenaeus* Smith; and *Artemesia* Bate. The fourth series contains *Macropetasma* Stebbing. This seriation is quite different from the generic groupings suggested by preceding workers (as Bouvier 1908). It is believed more nearly to express natural affinities.

The *Penaeus* series is characterized by the presence of three or more pairs of mobile but no fixed lateral spines on the telson, which also may lack an armature completely; THE PRESENCE OF VENTRAL ROSTRAL TEETH IN SOME OR ALL OF THE SPECIES OF ALL THE GENERA; AN ENTIRELY OPEN OR SIMPLE UNDIVIDED ENCLOSED SPERM RECEPTACLE; a simple open petasma; AN EPIPODITE ON THE THIRD MAXILLIPEDES; A PLEUROBRANCH ON SOMITE XIV.

The *Trachypeneus* series is characterized by the presence of a variable number of mobile lateral spines on the telson; a simple or complex enclosed sperm receptacle, which is always more or less completely divided into lateral halves; a SEMITUBULAR PETASMA WITH PRODUCED LATERODISTAL SPOUTLIKE CORNERS AND NO POSTERODISTAL PROJECTION; the absence of a pleurobranch from XIII, except in *Metapeneus*. All of the genera of the series, except the two that have heretofore been placed in "*Penaeopsis*," have either longitudinal or transverse sutures, or both, on the carapace.

The *Parapenaeus* series is characterized by THE PRESENCE OF ONE TO THREE PAIRS OF MOBILE LATERAL SPINES IN ADDITION TO A DISTAL FIXED PAIR ON THE TELSON; a simply invaginated pair of enclosed sperm receptacles; a simple open petasma or a SEMITUBULAR ONE WITH A PAIR OF SPINES OR LAMELLAE AT THE POSTERODISTAL MARGINS; A SPINE ON THE VENTROMEDIAN PROXIMAL MARGIN OF THE ANTENNULAR PEDUNCLE, which although present in the mysis of all Penaeidae and in the postmysis of Penaeinae, occurs in the adults of these three genera only of the family; the presence of a pleurobranch on somite XIII. In *Parapenaeus* there are longitudinal and transverse sutures of the carapace which are not present in the other two genera of the series.

Characters in small capitals are unique for each series.



*Macropetasma*, the single form here placed in a distinct series, resembles the Eusicyoninae in certain characters: the reduced series of thoracic exopodites, those of VII and X alone being present; the structure of the petasma; the subcoxal position of the male genital openings. In the first two characters mentioned, it also resembles certain members of the *Parapenaeus* series, from which, however, it differs strikingly by the absence of the median spine of the antennular peduncle, and by its telson armature of four pairs of mobile lateral spines. In these two characters it approaches the *Trachypeneus* series, which it likewise resembles in branchial formula, a pleurobranch being absent from XIII. The formula of VIII, which has been erroneously reported not to include a podobranch, is the same as that of all Penaeidae. The usual peneid armature of a spine on the distomedian margins of basis or ischium of the anterior legs is, as in *Artemesia*, completely lacking, although there is a tooth of the coxa of the first chelipeds, and a pair of curious opposed teeth on the basis of the third legs in the male. The thelycum appears to be unique, although, in the unavailability of enough material to permit dissection, I am unable to discuss the structure with absolute certainty: the anterolateral parts of sternite XIV seem to be elevated and folded over mediad so that each side encloses a sperm receptacle, in the formation of which the median plate of XIII plays no part.

#### PENAEUS Fabricius

The genus *Penaeus*, as restricted by the efforts of many workers, particularly Smith, 1886, and Alcock, 1905, includes to the present about twenty-four described species. Of these, however, two are forms closely related to *Funchalia*, as will be shown below, and the genus must therefore be further restricted by their exclusion. The twenty-one clearly characterized species (leaving for later consideration two doubtful African forms) may be divided into two subgroups, as follows:

##### Division 1

Adrostral carinae not extending to near the posterior margin of the carapace; postocular crest lacking: *P. setiferus* (Linnaeus), *stylirostris* Stimpson, *occidentalis* Streets, *vannamei* Boone, *semisulcatus* De Haan, *gracilirostris* Thallwitz, *caeruleus* Stebbing, *carinatus* Dana, *esculentus* Haswell, *indicus* H. Milne-Edwards, *merguiensis* De Man, *penicillatus* Alcock.

In all of these species the rostrum bears modally more than one ventral tooth; the telson is laterally unarmed; and the ischium of the first pair of chelate legs is armed with a spine.

## Division 2

Adrostral carinae reaching almost to the posterior margin of the carapace; postocular crest present: *P. brasiliensis* Latreille, *brevirostris* Kingsley, *marginatus* Randall, *canaliculatus* Olivier, *latisulcatus* Kishinouye, *plebejus* Hess, *mccullochi* Schmitt, *japonicus* Bate, *trisulcatus* Leach.

This division may be further subdivided on the character of the postocular crest, which turns upon itself at the posterior end, forming a loop, in the last five Indo-Pacific species mentioned and in the European *P. trisulcatus*. In the Indo-Pacific *P. marginatus* the character of this crest is not described (Rathbun, 1906), but the figure seems to indicate a loop. In the two American forms, *P. brasiliensis* and *P. brevisrostris*, the crest is simple, and indeed in the latter species it is often almost absent, as in division 1. In the five Indo-Pacific species and in *P. trisulcatus* the rostrum bears but one ventral tooth; in *P. marginatus* it is reported as regularly bearing more than one. In the American species, as in division 1, the rostrum bears more than one ventral tooth.

In the Indo-Pacific species, with the exception of *P. canaliculatus*, and in the European species, the telson bears a lateral armature of three pairs of mobile spines. In the two American species it is, as in division 1, unarmed.

In the Indo-Pacific species, with the exception of *P. marginatus*, the ischium of the first leg is unarmed. To me, it seems probable that the individual variants of *P. canaliculatus*, described by De Man, 1887 and 1911, as having ischial spines on the first chelipeds and the postrostral carina unsulcate, are actually to be referred to *P. marginatus*. The European *P. trisulcatus* is peculiar in exhibiting coxal spines on the first three legs, in addition to the basal spines of the first two which are universally present in *Penaeus*. In the American species the ischium of the first chelipeds, as in division 1, is armed.

There is, thus, in the American species of division 2, a correlation of four characters distinctive of division 1: incompletely developed postocular crest, more than one ventral rostral tooth, unarmed telson, and a spine on the ischium of the first legs. Only two of these characters mark *P. marginatus*; another is found in *P. canaliculatus*; none occur in the remaining species.

Three of the species of division 1 are set apart from the remainder of the genus by the lack of evagination of lamellae on somite XIV, such as enclose a sperm receptacle in the remainder of the genus. These three species, which display no other important differences from their group, except in a correlated difference of structure of the male

copulatory organ, are confined to America. Their open thelycum, which resembles that of *Funchalia*, seems to be primitive for the genus *Penaeus*, since the attachment appendages by which the spermatophores are fixed to the surface of the female sternites are present as apparently functionless rudiments in the remaining species, where the spermatophores are introduced into an enclosed receptacle. Of the other characters of subgenus 1 it is impossible to say whether or not the absence of a postocular crest is primitive for the genus. The presence of an ischial spine on the first cheliped is probably a primitive character, which is also found in *Funchalia*. The loss of a telson armature, and possibly the presence of more than one ventral rostral tooth, is a specialization. Short adrostral carinae are probably primitive. On the whole, division 1 appears to be less specialized than division 2, although to balance the retention of an open thelycum in some of its species, the probably specialized obsolescence of the subhepatic crest in others (*P. indicus* and related forms) might be cited. I am inclined to believe that, since the species of division 1 with open thelycum as well as the species of division 2 most nearly related to them are confined to America, an American origin is indicated for the genus.

The two species not included in the above discussion, which have been placed in *Penaeus* but whose relationships to the other forms are doubtful, are as follows:

1.—*P. durbani* Stebbing, 1917b, is incompletely described and figured. It is perhaps a normal member of subgenus 1, with enclosed thelycum.

2.—*P. pulchricaudatus* Stebbing, 1914, although its length of 40 mm. seems unusually great, is a postmysis form in what may be called the SICYNINE STAGE common to Penaeinae. It is altogether probable that this specimen is referable to a described adult of *Penaeus*, probably to *P. japonicus*.

Two species heretofore included in *Penaeus* (*P. balboae* Faxon, 1893, and *P. meridionalis* Lenz and Strunck, 1914) appear to be forms very closely related to *Funchalia* and, like it, adapted to a bathypelagic existence. The former was taken in the American Pacific; the latter, taken in the South Atlantic, was not compared by its describers with *P. balboae*, but is evidently very closely related to it. Alcock, 1906, has placed *Penaeus balboae* among the "uncertain and doubtful" members of the genus, but he states that, aside from the lateral spinelets of its telson, it adheres to the "*P. indicus* group" (a part of subgenus 1). The two species seem, however, to be very clearly set apart from an otherwise quite compact group of forms composing the genus *Penaeus*, especially by the modified carination of the carapace, consisting of three parallel longitudinal ridges, upon the intermediate of which the hepatic spine is borne, and between the intermediate and the lowest of which there is a

transverse connection; by the presence of many more than three pairs of lateral telson spines; by the presence of long antennular flagella; by the stylet-like form of the mandibular crown, and the absence, as in Eusicyoninae and all preadult, postmysis Penaeinae, of the fourth proximal endite of the internal lobe of the second maxilla. In these characters, the two species agree with *Funchalia*, save that the hepatic spine is not constantly present in that genus.

The branchial formula of *P. balboae* is identical with that of *Penaeus* and *Heteropenaeus*, and of *Funchalia* as emended by Calman, 1925, and as observed by me. Since *P. meridionalis* is figured as having a ventral rostral armature (the rostrum being broken in the holotype of *P. balboae*), which is lacking in *Funchalia*, and since the sculpture and armature of the carapace differ somewhat in the two species under discussion from that shown by *Funchalia*, I feel that *P. balboae* and *P. meridionalis* should be considered as forming the new subgenus **Pelagopenaeus** of *Funchalia*.

### Division 1

#### **Penaeus setiferus** (Linnaeus)

Figures 5 to 7

*Cancer setiferus* LINNAEUS, 1767.

?*Penaeus orbignyianus* LATREILLE, 1817.

*Penaeus fluviatilis* SAY, 1818.

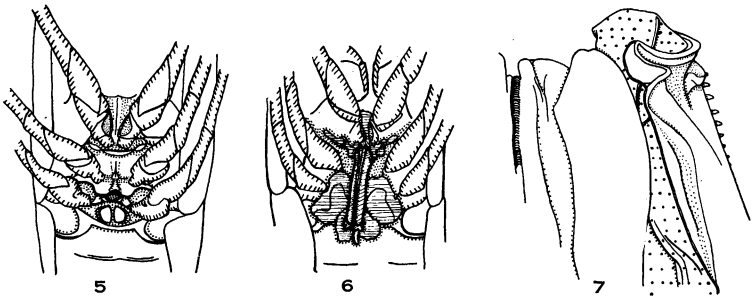
*Penaeus setiferus* H. MILNE-EDWARDS, 1837.

DISTRIBUTION.—*Penaeus setiferus*, the chief commercial crustacean of the Gulf and southern Atlantic coasts of the United States, and the most conspicuous of the Louisiana peneids, has been the subject of published mention since Seba, 1758. The species occurs over a considerable north-south range along the east coasts of the American mainlands but, as compared with the related *P. brasiliensis* Latreille, has a more restricted range and seems to have a more localized distribution within this range, although perhaps a greater local abundance. This distributional difference is probably the reflection of a more specialized adaptation to brackish water and rich estuarine feeding grounds in *P. setiferus* than in the latter, and perhaps in part to a higher optimum temperature requirement. *P. setiferus* seems to have been reported from Jamaica (Rathbun, 1897) alone of the Antilles, the Bahamas, and Bermuda. Unless *P. orbignyianus* Latreille from the Bay of Biscay is, as believed by Milne-Edwards, 1837, identical with *P. setiferus*, the species has not established itself in the eastern Atlantic. Between its Atlantic and its

Gulf range in North American waters the species seems to be absent from southern Florida.

**STRUCTURE AND NATURAL HISTORY.**—The largest specimen that I have taken is a female somewhat over 200 mm. in total length, with a carapace, excluding the rostrum, of 49 mm. Males do not reach the maximum size as often as do females, but there is apparently much less sexual dimorphism in size than is usual in Penaeinae.

The thelycum of *P. setiferus* has been described and figured by Andrews, 1911, who did not, however, perceive that it was functionally of a distinct type from that of *P. brasiliensis*, which he also described. The function of the free plates abutting on the median plate and enclosing



Figs. 5-7. *Penaeus setiferus* (Linnaeus).

5, thelycum; 6, thelycum with paired spermatophores attached; 7, petasma, left half, distal portion, ventral (posterior) surface.

a cavity in the latter species is easily recognized even when the cavity does not contain the spermatophores. On the other hand, the low-relief sculptures of the sternum of *P. setiferus*, in which homologues of the structures found in *P. brasiliensis* are perceptible, are not easily recognized as merely providing insertions for the attachment apparatus of the exposed spermatophores unless the latter are in position. The spermatophores of *P. setiferus* and the Solenocerinae have not been previously described, and the OPEN THELYCUM has consequently not been distinguished.

The thelycum consists of an unpaired protuberance on somite XIII, continued forward as a low ridge, and sloping posteriorly into an emarginate projecting plate which freely overhangs sternite XIV. This area is equivalent to the median plate of other peneid thelyca. The anterior part seems to develop from the buttress of a larval sternal spine. The posterior emarginate projection is represented by posterior and lateral less elevated parts of the median plate in other peneid thelyca. Anterior



to the median plate on XIII there is a cavity anteriorly demarcated by a high transverse ridge between the third legs and posteriorly margined by a transverse fleshy lamella. Although this cavity is of functional importance here, it plays no part in the enclosed thelycum of other penaeids, although the fleshy lamella is retained in other species of *Penaeus*. On sternite XIV, a low crescentic transverse ridge, interrupted in the midline and with its concavity directed forward, forms a posterior wall to a depression anteriorly overhung by the posterior margin of the median plate. This ridge seems to be homologous to the posterior lip of the transverse groove from which invaginated sperm receptacles are developed in other Penaeidae. Behind the ridge is a flat sternal area which bears a pair of rounded fleshy protuberances, one on each side of the median line. It may be noted that no evidence of seasonal or other changes in the structure of the adult thelycum was observed.

The spermatophores of a mature male are as follows: a large central demicylinder, in which the sperm mass is enclosed, is continued posteriorly (orientation as when attached to the female) as a flat vertical plate. Posterodorsally the demicylinder bears a thin horizontal lateral plate supporting a mass of glutinous material. At its anterior end the central part likewise bears on its dorsal margin a mass of glutinous material, as well as a slender laterally directed appendage. These attachment processes are the homologues of the spermatophore appendages described by Kishinouye, 1900, and by Mouchet, 1932, in species of *Penaeus* with an enclosed thelycum, where they seem to be no more than vestigial structures. Between the two attachment surfaces, the central part is bare. The spermatophore is constant in structure and lies completely formed in the enlarged lower end of the vas deferens of the male. The central part appears to be partly formed in the partitioned lumen of the middle part of the vas deferens, where a gelatinous secretion enfolds a column of spermatozoa. The constituents of this central part are received, the demicylinder molded and given its final sheathing, and the attachment structures secreted and added to it in the lower, enlarged part of the vas. The two spermatophores are evidently extruded with anterior end (with reference to the female) first. They are then fastened together, side by side, so perfectly that they appear as a bilaterally symmetrical unit, and are applied to the sternum of the female presumably through the agency of the petasma. The anterior glutinous masses are forced into the depression between the median plate and sternite XII, while a portion of the mass augments the strength of the hold by being forced between and in advance of the third legs. The lateral spurs

are placed in the space between the coxae of the third and fourth legs. The posterior glutinous mass is forced into the cavity between the anterior crescentic ridge of XIV and the posterior overhanging margin of the median plate; the remainder of the mass lies more or less securely anchored on the posterior surface of XIII. The main cylindrical sperm-carrying portion of the united spermatophores is elevated well above the sternum and extends from anteriorad the bases of the fourth legs to posteriorad those of the fifth. The spermatozoa consist of a flattened spherical head from which projects a short spike.

The petasma, on careful examination, proves completely adapted to holding the conjoined spermatophores in proper position for attachment. The cylindrical portions fit into the ventrally (posteriorly) directed concavity of the petasma. The elastic, unchitinized median portion of the two rami, hooked together by the cincinnulae of their median margins, serve as a cradle, while the rigid lateral margins of the petasma fix the spermatophore immovably into position by fitting into a longitudinal groove on its lateral surfaces dorsad the margin from which the attachment masses project. The anterolateral holdfasts of the spermatophore are locked into place at the distal end of the petasma by dovetailing into the rigid crenulations at the distolateral angles of the organ. The first pleopods are evidently swung far forward during sperm transfer, so that the petasma is pressed dorsally against the pereionic sternum of the male; and its ventral surface, from which the attachment masses of the spermatophore project, faces the thelycum of the female in belly to belly coupling.

The males appear to become sexually mature at a carapace length somewhere near 35 mm., or a volume of about 30 cubic centimeters, since although the length and especially the volume of the animal may increase considerably beyond this size, the spermatophores of larger individuals to not exceed the maximum dimensions attained at smaller sizes. It is a curious fact that ripe sperm first appear in very immature males of about 25 mm. carapace length, several molts before that which appears to represent maturity. Small spermatophores of simple platelike form are found at the lower end of the vas deferens of these immature animals, which with increase in size of the individual come to reproduce completely in form the large spermatophores of the adults. These preliminary spermatophores seem to be shed at each molt; but this point is difficult to determine. The small spermatophores of immature males are not found attached to females. Impregnated females are rarely found, are always fully adult, and, in all cases observed by me,

were taken near the outer limits of the inner littoral zone, which I interpret as meaning that mating occurs during the spawning migration. The elongated ovaries, which extend back to the end of the pleon, contain about half a million minute yellow eggs in large females. The eggs do not appear to have been mature in any of the specimens that I examined. Only a single specimen with possibly spent ovaries was observed among several thousand examined. Larvae of earlier than postmysis stages were never found within the inner littoral zone.

The species ranges from the almost fresh waters of the inland lakes and bayous more than a hundred miles from the Gulf of Mexico, through the inner littoral zone as far as twenty miles offshore. Although it undoubtedly migrates into the outer littoral or beyond, it has not yet been taken there. The perfluvial area investigated seems to support a more concentrated population than the coast to east or westward does. Although extreme local concentrations of individuals often occur, it is not certain that these represent true schools. The fact that segregation according to size is usual is not necessarily evidence of schooling, but may indicate a change in general tropic response with growth. Most of the individuals that may be taken in abundance in the inside waters are sexually immature. During the cold season this area is deserted. Both immature and mature individuals occur in the coastal area of the inner littoral zone, the population being composed chiefly of the immature during fall and winter. The spring and summer population is characteristically of large adults. In the fall adults are rarely found. As has been shown by Viosca, 1920 and 1923, the adults appear to grow to maturity in one year. I would interpret their disappearance as representing a departure from coastal feeding grounds on a spawning migration into the waters farther offshore.

Weymouth, Lindner, and Anderson, 1933, have stated that adults do not survive their second summer, death occurring after spawning. This important conclusion seems to rest upon an inadequate foundation. The fact that spent females are not discoverable (which I had pointed out to these workers) is hardly evidence that they have died; and indeed appears clearly to mean that knowledge of the later history of *P. setiferus* is completely lacking. Even though the adults should actually never reappear in the fishery, no evidence has as yet been presented to indicate that *Penaeus setiferus* may not spend a protracted adult life outside of the narrow coastal area investigated, in which circumstance individuals not available to the commercial fishery might form a breeding reservoir. The bionomic notes on *P. brasiliensis* presented in a suc-

ceeding paragraph offer a suggestive analogue. It may be noted that Kishinouye, 1900, states that the "large prawns" of *Penaeus* [*sensu stricto*] do not die after spawning, and that Heldt, 1931, does not mention the death in aquaria of *Penaeus caramote* after the eggs have been discharged.

Another statement of Weymouth and his associates, that the spawning takes place "within three weeks after the first appearance of the developing ovaries," aside from the fact that ovarian development appears to proceed regularly, without conspicuous sudden change, from the time of its inception in very immature individuals, seems to lack foundation. As spawning has not been observed, there is no evidence as to when in individual life the gonad is completely mature and is discharged. If the statement is based on the time of appearance of the larvae, it may be pointed out first that occurrence and specific determination of larvae have not been discussed by the investigators concerned, and further, that a correlation of the first appearance of larvae with the observable, probably incomplete, progress of maturation of the ovary in coastal adults, would be of uncertain significance.

A more extensive discussion by Weymouth, Lindner, and Anderson (1933, Bull. U. S. Bur. Fisheries, XLVIII), of their studies of the life history of *Penaeus setiferus* has appeared since the foregoing was written.

In regard to the standard measurement selected by Weymouth and his collaborators, it may be stated that the study of standards to which they appear to refer (*op. cit.*, p. 8) indicated that the total length measurement cannot be accepted as a criterion of size without critical interpretation. When this standard is used for expression of growth changes, the decrease in relative length of the rostrum with increasing size should appreciably, even though only to a small extent, offset actual growth increases. The comparison of Atlantic material with gulf shrimp of larger size is likely to occur unless compensation is made for the longer rostrum of the Atlantic population. Finally, volumetric measurements indicate that certain important changes in actual size are not reflected in total length.

It is unfortunate that the authors (*op. cit.*, p. 7), while reviewing those portions of his work to which Viosca had attached less emphasis, have neglected to mention his major contributions in the papers quoted: namely, those dealing with growth, which are approximately coincident with their own conclusions. The criticism of Viosca's statements of preadult history offered by the Bureau of Fisheries' investigators (*op. cit.*, p. 17) appears to rest on a basis little more secure than that of the

intelligibly erroneous conceptions criticized. Viosca's belief that larvae are planktonic up to a large size is based on the occurrence of a large and abundant planktonic penaeine postmysis, evidently overlooked by Weymouth, *et al.*, which is not distinguishable from the early postmysis stages of *P. setiferus* by conspicuous morphological differences other than size. The postmysis stages of *P. setiferus* are not "essentially similar to the adult except in size" (*op. cit.*, p. 15) and they may be found outside of the estuarine area.

No absolute determinant of male ripeness, such as the presence or absence of spermatophores, stated by these workers (p. 13) to have been employed, is possible. Immature males with ripe spermatozoa and structurally perfect spermatophores are present at all seasons of the year; the denial (p. 16) that Kishinouye's findings apply to *P. setiferus* is in error. Likewise, although the criteria of female maturity employed are not described, from the statement that more than one-seventh of the females observed to be in the "last stage of ovary development recognized" were found in inside waters, I presume either that the standards were inadequate or that the Georgian population differs in behavior from the Louisianian. The ova, by the time of impregnation, do not appear to attain more than two-thirds the diameter given by Weymouth and his co-authors (*op. cit.*, p. 6).

The assumption (*op. cit.*, pp. 12, 13) that spawning must occur within a few hours of impregnation is both unwarranted and improbable; the spermatophores can be dislodged only with considerable difficulty.

Statements by Weymouth, Lindner, and Anderson as to period and location of spawning are supported by no better evidence than are the conclusions of Viosca, which they regard as being without adequate foundation. The statement ". . . they spawn and disappear . . ." (*op. cit.*, p. 7) is unwarranted and probably erroneous, inasmuch as the disappearance, which had been observed as far back as Spaulding, 1908, occurs without there being any indication that these individuals have already spawned.

As to the fate of adults, the disappearance, even the permanent disappearance, of adults from the narrow littoral zone occupied by the fishery is hardly to be regarded as equivalent to a "short life span of one year" (*op. cit.*, p. 22), so long as there is no evidence that the adults, after a preliminary littoral life, do not occupy an offshore range. The statement "as we have seen, *P. setiferus* appears to be absent from deep water" (*op. cit.*, p. 23) assumes the point, inasmuch as the authors have



not presented any evidence that *P. setiferus* does not occur offshore from the limited region that they have explored.

The geographical range given as that of *P. setiferus* (*op. cit.*, p. 23) refers to *P. brasiliensis*.

VARIATION WITHIN THE SPECIES.<sup>1</sup>—Specimens of *P. setiferus* available to me, from localities other than Louisiana, were fourteen large females and six large males (carapace length from 33 to 39 mm.) from North Carolina, and a large male from Fire Island, Long Island, New York (which seems to represent the extreme northern record), in the collection of the American Museum; a large male and female from South Carolina loaned by the Philadelphia Academy; six specimens from South Carolina and one from North Carolina, in the collection of the Peabody Museum of Natural History at Yale. A comparison of the North Atlantic specimens with a considerable Louisiana series of equivalent size showed the former to differ somewhat from the Gulf coast stock.

In large Atlantic specimens, the rostrum always extended beyond the antennular peduncle, often by 5 or 6 mm.; the Louisiana specimens it sometimes did not exceed the peduncle, and rarely exceeded it by as much as 4 mm.

The third legs of Atlantic specimens often fell short of the tip of the antennal scale, and seldom exceeded it by as much as half the dactyl; the third legs of Louisiana specimens more rarely fell short of the scale, and quite usually exceeded it by half the dactyl or more.

The petasma of Atlantic specimens, though not differing conspicuously in form, is shorter at any given size, as measured along its lateral margins, than that of Louisiana males.

These proportional characters are variable with change in size of the individual. Thus, the length of the petasma appears to increase regularly with increase in the size of the individual. The rostrum in Louisiana specimens decreases in length, as compared to the antennular peduncle, in direct ratio to increase in size. The third legs seem, to some extent, to increase in length proportionate to the antennal scale in direct ratio to increase in size. Therefore, the longer rostrum, shorter third legs, and shorter petasma of North Carolina specimens as compared with those of Louisiana are perhaps to be regarded as simply indicating the attainment of as great a size in the former as in the latter at a less advanced developmental stage. Such a difference in the correlation between size and instar might be determined directly by environment

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<sup>1</sup>Material regarded by previous investigators as *P. setiferus*, from Jamaica and Brazil, seems quite distinct from the North American form. A description of southern specimens recently obtained by the Bingham Oceanographic Collection is in preparation.

and need not indicate a racial difference between the stocks of the two localities.

In one character, however, the Atlantic stock seems to differ from Louisiana stock without reference to size. The postrostral carina of *Penaeus setiferus*, behind the epigastric tooth, is interruptedly grooved longitudinally for a short distance. The chief part of this sulcus appears as a posterior concavity leading by a constricted groove of variable breadth to an anterior one, which is continued toward the epigastric by a narrower and shallower line. In Atlantic specimens, the constriction between the anterior and posterior parts is usually only slightly marked, and the tapering sulcus in advance of the anterior portion is readily perceptible. In Louisiana materials, the entire sulcus is usually narrower, the constriction between the two parts often so great as to constitute an interruption of the sulcus, and the anterior part usually ends abruptly without a tapering prolongation. This difference perhaps represents a racial difference between the two stocks, which would imply a segregation, with some lack of intermixing dispersal along the coasts, of commercially important stocks of *P. setiferus*.

RELATIONSHIP TO OTHER SPECIES.—*Penaeus setiferus*, by its open thelycum, is clearly distinguished from all other members of the genus except its three Pacific American congeners, *P. stylirostris* Stimpson, 1871, *P. occidentalis* Streets, 1871, and *P. vannamei* Boone, 1931.

Much confusion has involved the west-coast species from the time of their description to the present. Stimpson's types were lost even before the publication of his description; while within a month after, and possibly even before the appearance of Stimpson's work, an independent description of a very closely related species from the same locality, Panama, was published by Streets. Streets' description was hardly of a nature to differentiate his species from that recognizably described by Stimpson, and his types appear to have included a specimen of *P. stylirostris* (the largest individual, mentioned as with long antennular flagella). The next event in the history of these species was the relegation of one of them by Miers, 1878, to the synonymy of *P. indicus*; this error was corrected by Miers himself in 1885, at which time he reasonably suggested that Streets' species might be a synonym of Stimpson's. This latter view was tentatively accepted by De Man, 1911, who attributed it to Rathbun. Rathbun, 1910, appears (according to the rostral formulae cited) to have included both *P. stylirostris* and *P. occidentalis* from Peru under the former name; the figured individual, however, is correctly determined. The most recent writer, Boone, al-

though her types actually represent a species distinct from the two previously named, has not distinguished *P. vannamei* from its relatives by any diagnostic character. Indeed, the "*P. stylirostris*" with which Boone compares the new species is *Xiphopeneus kroyeri* variety *riveti* Bouvier. *P. occidentalis* is figured by Boone, but not compared with *P. vannamei*, under the name "*P. brevirostris*."

It therefore seems safe to state that the existence of three distinct species of the *P. setiferus* group on the Pacific American coast has not been previously suspected. This fact is remarkable in that all three species attain a very considerable size and are sufficiently abundant to support an extensive fishery; they are regularly sold in the markets of Panama City, and are shipped across the isthmus to be sold together with locally caught *P. setiferus* in Colon.

Material examined by me has included the type of *P. vannamei* Boone and the paratypes, together with three other specimens from Sinaloa, Mexico, labeled "*P. stylirostris*," contained in the collection of The American Museum of Natural History; type material of *P. occidentalis* Streets made available by the Philadelphia Academy of Natural Sciences; a number of specimens of *P. occidentalis* from Panama in the collection of The American Museum of Natural History and of the Zoölogy Department of the Peabody Museum of Natural History at Yale; and several specimens of *P. stylirostris* Stimpson in the collection of the Zoölogy Department of the Peabody Museum.

During a recent expedition of the Bingham Oceanographic Foundation, an extensive collection of all three species was obtained at Bella Vista Beach, Bay of Panama. Detailed morphological study of this material has not been completed. Certain field observations may be of interest: Unripe adults of *P. stylirostris* and *P. occidentalis* attaining more than 250 mm. total length were taken in considerable abundance by seine, early in February, within one hundred feet of the shore in water up to about ten feet deep. The temperature of the water was very low in comparison with that of the air. The bottom was of silt and fine sand, and like certain of the Louisiana fishing-grounds for adult *P. setiferus*, appeared to support as its chief "vegetation" a large *Bougainvillea* trophosome and a *Bowerbankia*-like bryozoan. Sharp changes in predominance from one to the other shrimp, in consecutive hauls from the same locality, suggested that the two species might move in pure aggregations, a possibility of interest in connection with the problem of whether peneid aggregations may be true schools. *P. vannamei* was much less abundant than the other two species and did not attain so large a size, but the

material observed appeared not to be fully adult. Some quantity of juveniles of all three species, but particularly of *P. occidentalis*, was taken with the adults.

The only record of the group from north of Panama known to me is of *P. vannamei* from Mexico. It seems possible, since this species was, conversely, less abundant than its congeners at Panama, that it has a more northerly center of distribution than *P. stylirostris* and *P. occidentalis*.

An incomplete preliminary statement of the characters distinguishing the four species of the *setiferus* group is as follows:

*P. vannamei*, rostral teeth usually  $\frac{1}{2}$ ; adrostral carinae conspicuously shorter than in the other two Pacific species, and somewhat shorter than in *P. setiferus*, usually not reaching behind the epigastric tooth. Carina ventrally bordering the lateral sulcus which accompanies the median dorsal carina of the sixth pleonic somite higher and distinctly sharper than in the other three species. Thelycum: posterior part of sternite XIV without sculpture; anterior part with a pair of lateral prominences connected by a low arc-shaped ridge, equivalent to the crescentic ridge of *P. setiferus*. Posterior margin of sternite XIII, which does not project free over the following somite, is shallowly emarginate. Anteriorly from the posterior margin of XIII a very conspicuous cusp slopes up, the semicircular anterior margin of which is sharply elevated above the general level of the sternite.

*P. occidentalis*, rostral teeth usually  $\frac{10}{8} - \frac{11}{4}$ ; rostrum distally unarmed above for less, usually much less, than one-third its length. Antennular flagella subequal in length, about one-third shorter than the peduncle. Thelycum: Sternite XIV with a very low median longitudinal crest which disappears anteriorly and is overlapped in adults by the swelling of the areas lateral to it, which at the same time become densely setose. These areas occupy almost the entire sternite and are perhaps equivalent to the much smaller fleshy protuberances of *P. setiferus*. No trace of crescentic ridge save for a pair of very faintly elevated anterolateral pubescent areas in juveniles. Posterior margin of XIII deeply but broadly emarginate, not projecting free. Somewhat behind the middle of the sternite is a fairly high oval projection sloping gently into the surrounding surface.

*P. stylirostris*, rostral teeth usually  $\frac{1}{4}$ ; rostrum distally unarmed above for about one-half its length. Inferior antennular flagellum more than twice superior in length, about one-third longer than peduncle. Thelycum: Posterior part of sternite XIV with very conspicuous, high, blunt, median longitudinal ridge. No trace of the paired fleshy protuberances or the crescentic ridge. Posterior margin of sternite XIII not projecting free, almost straight, and with a small median convexity. Posterior portion of XIII with a low median longitudinal ridge extending anteriorly, to end in a well-marked transverse carina probably equivalent to the high lamella of *P. setiferus*.

*P. setiferus*, rostral teeth usually  $\frac{1}{2}$ , rostrum usually unarmed above for about its distal half. Superior antennular flagellum somewhat longer than inferior, less than one-third shorter than peduncle; basal portion of inferior flagellum of adult male flattened in the vertical plane and with a conspicuous dorsal row of spines. Thelycum distinguished by the pair of small fleshy protuberances and the strong

crescentic ridge of XIV; and the free posterior margin, very faint median carina, and high transverse anterior lamella of XIII.

There are a number of other well-marked differences between the four species, especially in shape and size of the coxal projections of the three posterior pairs of walking legs of the female, and in petasma.

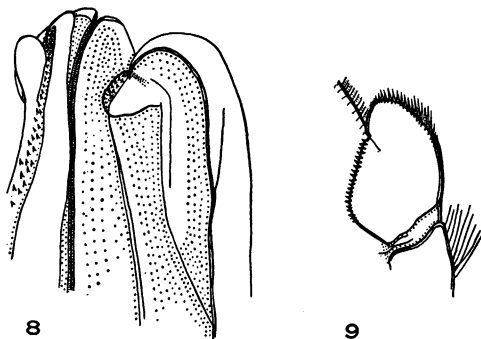
## Division 2

### ***Penaeus brasiliensis* Latreille**

Figures 8 and 9

*Penaeus brasiliensis* LATREILLE, 1817.

DISTRIBUTION.—*P. brasiliensis* seems to occur quite generally over a north-south range somewhat greater than that of *P. setiferus*, from about 41° north to 32° south latitude on the east coasts of the Americas. It has been reported from many of the Antilles, the Bahamas, and



Figs. 8-9. *Penaeus brasiliensis* Latreille.

8, petasma, distal portion, ventral (posterior) surface, left endopod spread; 9, appendix masculina of left second pleopod, anterior surface.

Bermuda, and is established on the West African coast. The record by Boone, 1930, from the Mediterranean probably refers to *P. trisulcatus*.

In several parts of their range, as on the North Atlantic coast of the United States, *P. brasiliensis* is more abundant than *P. setiferus*; but in Louisiana, where the latter reaches its climax of abundance, *P. brasiliensis*, although apparently as numerous as in other parts of its range, is relatively inconspicuous. The difference in distribution seems to rest partly on the lesser dependence of *P. brasiliensis* on brackish estuarine feeding grounds, as indicated by the bionomic data set forth below.



STRUCTURE AND NATURAL HISTORY.—The largest female taken was of about 195 mm. in total length, with a carapace of 47 mm. The largest male had a total length of 142 mm. and a carapace of 31 mm.

The thelycum is of a simple enclosed type. The median plate consists of a transverse ridge on the anterior part of somite XIII, which does not possess the functional significance of the probably homologous fleshy transverse ridge of *P. setiferus*. The posterior part of the sternite bears a high boss merged behind with a prism-shaped prominence with a concave ventral surface, the entire structure being homologous with the longitudinal ridge of somite XIII in *P. setiferus*. The posterior margin of XIII projects as a deeply emarginate shelf upon which the lips of the receptacle of XIV abut. On somite XIV a U-shaped elevation whose apex is near the posterior median margin of the sternite surrounds a depressed area. The arms of this elevation end anteriorly on each side, and the inner margins of the elevation are produced as two paired plates which meet but do not join in the midline. These "lateral plates" enclose above them an undivided sperm receptacle. Their median margins are in adults thickened and raised. The spermatophores are evidently inserted into the cavity above the plates through the median longitudinal slit between them. It has been observed by Heldt, 1931, that in *P. trisulcatus* the sperm from the disintegrated spermatophore finds egress by dorsoanterior openings formed on either side of the median plate by the gaps between this and the anterior margins of the lateral plates. This egress, in *P. brasiliensis*, is guarded by the wedge-shaped expansions of the coxae of the fourth legs. This type of thelycum is modified in *P. japonicus*, by the median fusion of the lateral plates or, more probably, by the shifting forward of the posterior margin of the U-shaped elevation, so that the opening of the receptacle becomes anterior and transverse.

The spermatophores seem to be provided with rudimentary anchoring appendages, such as are functional in *P. setiferus*; but the heavy external coating and the well-defined structures of the exposed spermatophore are here no more than remnants. The petasma is strongly laterally compressed, with rigid lateral margins distally smoothly curved and apposed behind the ski-like tips of the median portions. This petasma is clearly adapted to entering the median slit of the thelycum. It is probable that the two soft spermatophores are received from the genital apertures and fitted together within the copulatory organ before being introduced into the receptacle. Surface and sectional views of the

thelycum of *P. brasiliensis*, with and without enclosed spermatophores, are given by Andrews, 1911.

Sexually mature adults have been taken only beyond the coastal area of the inner littoral zone in Louisiana, the species in this differing from *P. setiferus*. In other localities adults of both species seem to occur together. The spawning grounds are perhaps nearer shore than those of *P. setiferus*, since a concentration of sexually active adults was found in the outer littoral zone where *P. setiferus*, presumably still scattered in migration, has not been found.

Small, sexually immature individuals are present in some abundance in the coastal area and the inside waters during the summer months. They are usually, though not always, taken in company with young *P. setiferus*. They are relatively more abundant in the higher salinities west of the Mississippi than in the Mississippi Sound and Louisiana Marsh east of it, but are found even in the almost fresh waters of such lakes as Pontchartrain, more than a hundred miles from the Gulf. The entire coastal and inside population of small, immature individuals is of a brownish-gray color, and the sexes are almost equal in size and number. Farther from the coast larger individuals with a yellowish tinge are to be found. In the outer littoral zone thirty miles off Barataria Pass, on relatively barren shell bottoms, a fairly concentrated population was found which was brilliant translucent orange-yellow in color, the large blue chromatophores of the inshore specimens here being much reduced in size and number. The maximum size of males was greater than in the inshore population, that of females very much greater; the minimum sizes of both sexes seemed slightly above the usual inshore maximum. Females were much more numerous as well as much larger than males. Many of the larger females were impregnated. It would appear from the above that adults do not return to the more coastal waters; that the postlarvae pass their preadult life in the estuaries, later moving offshore to mature, and there losing the coloration adapted to a shallow water existence. Should the disparity in sex ratio between inshore and offshore populations be confirmed by examination of a greater quantity of material, the most probable interpretation would appear to be that the offshore females live for several seasons while the males are reduced in number by an earlier death.

VARIATION WITHIN THE SPECIES AND RELATIONSHIP TO OTHERS.—*P. brasiliensis* and its Pacific-American congener *P. brevirostris* are, as shown in a preceding section, quite distinct from the other species of division 2. Their nearest relative is the Hawaiian and possibly East Indian *P.*

*marginatus* which appears to differ by its armed telson, looped post-ocular crest, and unsulcate postrostral carina. *P. canaliculatus*, which resembles the American species in its unarmed telson, otherwise differs from them in the same way as to other Indio-Pacific species. The Mediterranean and eastern Atlantic *P. trisulcatus*, whose range overlaps that of *P. brasiliensis* on the African coast, is uniquely distinguished from the American species, in addition to the usual characters, by the armed coxae of its chelipeds.

*P. brevirostris* was named as distinct from the Atlantic *P. brasiliensis* by Kingsley, 1878, who in 1879 declared the two species identical. *P. brevirostris* was erroneously placed in the synonymy of *P. canaliculatus* Olivier by Holmes, 1895. In 1900 the same author recognized his material as distinct from *P. canaliculatus* and named it *P. californiensis*. This name has been placed in the synonymy of *P. brevirostris* by Rathbun, 1902 and 1904, and Schmitt, 1921, who consider the Pacific form to be distinct from that of the Atlantic. The distinctions between the two species, according to the above investigators, are as follows:

In *P. brevirostris* (1) the rostrum is higher than in *P. brasiliensis* and is shorter, not reaching to the end of the antennular peduncle; (2) the legs are shorter and stouter, the third legs reaching only to the apex of the antennal scale; (3) the grooves beside the postrostral carina extend nearer the posterior margin, and posteriorly are parallel rather than convergent; (4) the thelycum and petasma are different (differences not defined).

The diagnostic value of the above distinctions and the variation occurring within the Atlantic species may be discussed together. In differentiating *Penaeus brasiliensis* from *P. brevirostris*, Rathbun, 1902, states that the rostrum of the former exceeds the antennular peduncle in large individuals. It is, however, not so described by Rathbun, 1901, Hay and Shore, 1918, or De Man, 1925, all dealing with fairly large specimens, while I find that in Louisiana material the rostrum varies from a length not exceeding the second segment of the antennular peduncle, to somewhat beyond the end of the peduncle in a few small specimens. There seems to be a decrease in length of rostrum relative to antennular peduncle in direct ratio to increased size of the specimens, large individuals having shorter rostra than small ones. No conspicuous differences in rostral length between materials from different Atlantic localities were discernible. A comparison with specimens of *P. brevirostris* indicates that although the rostrum of the latter is usually shorter than that of the Atlantic species, the character is not diagnostic. The rostral crest is not higher in *P. brevirostris* than in *P. brasiliensis*, but the tip is quite often more depressed, giving a higher appearance to the supra-

marginal portion. The dorsal rostral teeth of *P. brasiliensis* are described by Benedict, 1894, and De Man, 1925, as numbering ten in West African specimens, but two specimens from Banana, Belgian Congo, which I have examined, have only nine teeth. In the American Atlantic, by all accounts and by an examination of material from Colombia, Louisiana, and North Carolina, the number of teeth is variable, with nine the mode. No marked local differences in the frequency of numbers of teeth were discernible, but the quantity of specimens available from localities other than Louisiana was not great enough to make slight differences in ratio of variation apparent. It is possible that *P. brevirostris* may have a different modal number or frequency in number of dorsal rostral teeth from that of Atlantic material, but such is not apparent in the ten available specimens. The anteriormost of the (usually) two ventral rostral teeth is described by De Man, 1925, and figured by Milne-Edwards and Bouvier, 1909, as opposite or anterior to the anteriormost dorsal tooth. I find this tooth to vary in its relation to the dorsal one, from before to well behind it. Such variation in position likewise occurs in *P. brevirostris*, so that the difference noticeable between the descriptions of *P. brasiliensis* mentioned above and the figure of *P. brevirostris* by Holmes, 1900, in which the inferior is placed behind the superior tooth, is not significant.

The median sulcus of the postrostral carina, which may be regarded as equivalent to an expansion of the two or three discontinuous shallow depressions observable in the carina of the species of division 1, is variable in distinctness in *P. brasiliensis*. In Louisiana specimens of all sizes down to very small ones, it is continuous and distinct. In Colombian examples of from 17 to 9 mm. in carapace length, this groove is usually narrow, often indistinct and discontinuous, or even almost absent. In *P. brevirostris* the sulcus is well marked. The adrostral sulci accompanying the postrostral carina are quite variable in length and breadth. In Louisianian, African, Cuban, and North Carolinian specimens of all sizes, they may be termed broad. In specimens from Colombia and Jamaica they are by contrast very narrow. In *P. brevirostris* they lie between these two breadths. Their outline in Atlantic materials is highly variable; they by no means always "converge posteriorly" as stated by Rathbun, and are not at all clearly distinguishable from those of *P. brevirostris*. Their length, as determined by their extent toward the posterior margin, seems somewhat variable. Indeed, although Rathbun says that they reach nearer the posterior margin in *P. brevirostris* than in *P. brasiliensis*, in my material the opposite seems true.

In degree of approach to the anterior margin made by the orbito-

antennal carina, and in sharpness of the postocular crest, all Atlantic material seems constant. In Pacific specimens, however, these characters are individually variable and the carina is often clearly shorter than in *P. brasiliensis*, the crest often hardly distinguishable.

The third legs of *P. brasiliensis* are quite variable in length, even in a homogeneous sample, and it is only of Louisiana specimens that enough material was available for a determination of the modal length. From the other material available for thorough study, five very large specimens from North Carolina and ten small ones from Colombia, it seems possible that local differences in this character may be clearly marked. The third legs of these specimens are shorter than those of Louisiana specimens of comparable size; whereas they are, to about the same degree, longer than those of *P. brevirostris*. Thus, though the third legs of *P. brevirostris*, not extending beyond the antennal scale, are short when compared with Louisiana materials (in which the leg, although ranging down to shorter than the scale, often extends beyond it by a considerable portion of the carpus), they are not very short when compared to Colombian specimens in which the leg does not usually much exceed the scale. The third legs appear to vary in proportionate length with change in size, being relatively as well as actually longer in larger individuals.

The thelycum of *P. brasiliensis* is not greatly variable except with growth changes. Although the figures published by Ortmann, 1890, of a Brazilian specimen, and by De Man, 1925, of a West African female differ considerably in the proportion and outlines of the parts, it seems improbable that the difference is significant. There is some individual variation in the shape of the lateral plates and in the dimensions and sculpture of the median plate, but I can find no clear local distinctions. The thelycum of *P. brevirostris*, although stated by Rathbun to differ from that of *P. brasiliensis*, seems to me to fall within the range of the latter.

It thus appears that the differences between the Atlantic and Pacific species in the above characters are not excessively greater than those between what appear to be differentiable local races of the former. There are two further characters, however, in which the Pacific is clearly if minutely distinct from all Atlantic material examined. These are, first, that the tips of the lateral and median lobes of the distal end of the petasma of *P. brevirostris* are acutely pointed, and, second, that the external margin of its appendix masculina is concave.

It may be mentioned that I have seen no specimens of *P. brasiliensis* that resemble in certain characters the figure published by Milne-Edwards

and Bouvier, 1909, in which the unarmed tip of the rostrum is very short, the cervical sulcus extends far dorsad, the posterolateral margins of the fourth and fifth pleonic segments are of peculiar shape, and the cicatrices on the sides of the sixth pleonic segment overlap. These cicatrices of *Penaeus* may be noted as probably representing the discontinuous remnants of a longitudinal lateral carina such as occurs in *Funchalia* and other peneids.

The antennae of specimens from various localities, although variable, seemed at least no shorter than the minimum figure, seven times the carapace minus the rostrum, by which Ives, 1891, distinguishes the "variety" *P. b. aztecus*, which until other distinguishing features are found, may be dropped.

#### TRACHYPENEUS Alcock

The genus *Trachypeneus* is separable into two divisions, as follows:

##### Division 1

Epipods are present on the first and second pairs of walking legs (in addition to those present on the third legs throughout the genus). The thelycum consists of a pair of invaginated sperm sacs whose apertures are continuous medially with the opening of an unpaired pocket into which sperm-free male secretion is received.

##### Division 2

Epipods are absent from the first and second legs. The unpaired pocket appears to be absent.

The second division is confined to the Indo-Pacific. I have not examined any material of it. Representatives of the first subgenus occur in Indo-Pacific and American waters and may be separated into two groups as follows:

SECTION 1.—Longitudinal suture extending well behind the hepatic spine; basis of the third maxillipeds armed with a spine; ischium of the first legs unarmed, the posterior lips of the transverse groove from which the unpaired pocket is invaginated are produced as a pair of free flaps. The members of this section are the Atlantic-American *T. constrictus* (Stimpson) and *T. similis* (Smith), an undescribed Pacific-American species, and an undescribed Pacific-American variety of the Atlantic *T. similis*.

SECTION 2.—Longitudinal suture not extending behind the hepatic; no spine on the basis of the third maxillipedes, ischium of the first legs armed with a spine. The posterior lips of the transverse groove are not produced. To this section belong the Indo-Pacific *T. curvirostris* (Stimpson) and related or identical forms, and an undescribed Pacific-American species.

Schmitt's statement (1926a) that "as regards . . . carapace . . . [the Pacific representatives of *Trachypeneus*] are so very much alike within reasonable variational limits as to render detailed descriptions of their

appearance rather superfluous," leaves out of consideration the important diagnostic character, length of longitudinal suture, which Schmitt neither describes nor figures in this paper quoted, nor for *T. pescadoreensis* Schmitt, 1931. Beyond the information given by De Man for *T. salaco*, in which it is completely absent, there is apparently no account available of this structure among the somewhat confused species of division 2.

*Trachypeneus*, *Xiphopeneus*, *Parapeneopsis* and *Atypopeneus* form a homogeneous group of genera in which a pleurobranch is absent from both somites XIII and XIV, and the carapace bears either longitudinal or transverse sutures or both. The cosmopolitan *Parapeneopsis* is very close to division 2 of *Trachypeneus*, especially in the characters of its thelycum, and is clearly distinguishable only by the fact that epipodites are constantly absent from its third legs. The American *Xiphopeneus* is very close to division 1, section 2 of *Trachypeneus*, in the characters of its thelycum, but is distinguishable from this group and from the related genera by several characters, especially by the elongation and subdivision of the dactyls of the last two pairs of legs and the absence of a transverse suture. In these first three genera mentioned, the spermatozoa are organized into numerous minute subspherical spermatophores. I have not examined specimens of *Atypopeneus*, which is confined to the Indo-Pacific. This genus seems to resemble somewhat *Parapeneopsis* in the form of its thelycum. The lateral parts of the transverse groove of its thelycum are, however, much elongated, and the entrances to the receptacles are closely approximated rather than well separated. It appears to be clearly distinguishable from all of the three preceding genera only by the absence of a buttress at the base of the antennal spine of its carapace. From all except the female of *Parapeneopsis maxillipedo* Alcock (1906), *Atypopeneus* is distinguished by the presence of a spine on the basis of its third legs; from all except *Trachypeneus salaco* De Man and perhaps the other members of division 2, by the complete absence of a longitudinal suture; from all except *Xiphopeneus* and some species of *Parapeneopsis* by the complete absence of lateral spines from its telson.

Two of the species which have heretofore been merged in the "genus" *Penaeopsis*, "*P.*" *mobilispinis* (Rathbun) and "*P.*" *richtersii* (Miers), lack a pleurobranch on somite XIII and form a fifth genus of the *Trachypeneus* series, in which both longitudinal and transverse sutures are completely lacking. The thelycum is much like that of *Atypopeneus*.

Approximately twenty species related to "*P.*" *affinis* H. Milne-Edwards, heretofore included in "*Penaeopsis*" but which may be distinguished as *Metapeneus*, form a second genus in which both transverse and

longitudinal sutures are absent, apparently related to the *Trachypeneus* series. Although these species bear a pleurobranch on XIII, and although their sperm masses are not organized into minute packets, they seem to be distinct from the third genus which has been lumped under the name *Penaeopsis* by their lack of a pterygostomian or branchiostegal spine, and of a spine on the mediobasal margin of their antennular peduncle; the presence of mobile but no fixed lateral teeth on their telson; the produced gutter-like lateral cornua of their petasma which lacks posterodistal projections; and the presence of a spine on the basis of their third legs. Their thelycum is much like that of *Atypopeneus*.

#### Division 1, Section 1

#### **Trachypeneus similis** (Smith)

Figures 10 and 11

*Parapeneus constrictus* variety *similis* SMITH, 1886.

*Parapeneus similis* RATHBUN, 1901.

*Trachypeneus constrictus* variety *similis* ALCOCK, 1906; MILNE-EDWARDS AND BOUVIER, 1909; DE MAN, 1911.

*Trachypeneus constrictus* CARY AND SPAULDING, 1909.

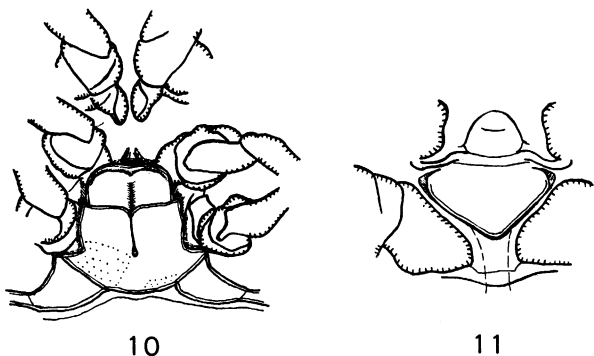
DISTRIBUTION.—*Trachypeneus similis* of the Atlantic, although recognized as not completely identical with *T. constrictus*, has not in the past been carefully distinguished from that species. In particular, the record of *T. constrictus* from western Louisiana by Cary and Spaulding, 1909, based upon a determination made by the United States National Museum, is erroneous, since an examination of the material shows it to be referable to *T. similis*. *T. constrictus* does, nevertheless, occur in eastern Louisiana, but it is much less frequently taken than is *T. similis*. A careful redetermination of a quantity of material in the collections of The American Museum of Natural History, the U. S. National Museum, the Peabody Museum of Natural History at Yale, and the Bingham Oceanographic Foundation, indicates the distribution of the two species to be as follows:

*T. constrictus* alone occurs on the Atlantic coast of the United States, as far north as Chesapeake Bay. Both species occur in the northern Antilles, the western coast of Florida, and Louisiana. *T. similis* alone is known from Venezuela, the type locality. The relative abundance of specimens from localities where both were present is in agreement with the conclusion that the center of distribution of *T. constrictus* lies to the north and east of that of *T. similis*, and that the former is replaced by the latter species on the western and southern shores of the Gulf of



Mexico and the Caribbean. A form so closely related to *T. similis* as to constitute no more than a variety occurs in the Gulf of California, but no representative of *T. constrictus*, which perhaps indicates that the absence at present, so far as is known, of *T. constrictus* from the Mexican-Central American east coasts was also true of past geological time. I believe it probable that *Trachypeneus similis*, but not its ally, will be found to occur on the Atlantic coast of South America.

*Trachypeneus similis*, *T. constrictus*, or other members of the genus, have not been recorded from the eastern Atlantic. *T. constrictus africanus* Balss seems, as noted by Schmitt, 1926b, a misnomer for *Parapeneopsis atlantica* Balss.



Figs. 10-11. *Trachypeneus similis* (Smith).

10, thelycum of impregnated female; 11, male pereopod sternites XIII and XIV.

**STRUCTURE AND NATURAL HISTORY.**—The largest female taken had a total length of 87 mm.; the largest male, of 44 mm. Females were very much more numerous than the rare and diminutive males. The species although not uncommon, was a relatively minor part of the peneid population. It was taken in depths of from five to fifteen fathoms in the inner littoral zone along the entire coast investigated, both east and west of the Mississippi River.

The thelycum of *T. similis* is extremely complicated. It appears in simple form in young females as a deep transverse groove in the anterior part of sternite XIV, the posterior lip of which embraces the posterior and lateral margins of the raised median plate of sternite XIII. Later, a dorsoventrally flattened invagination is pushed back beneath the integument of XIV from the median portion of the groove, while the posterior lip of this portion of the groove recedes from the median plate. The lip becomes produced on either side of the median line into a flap that forms

an anterolateral cover continuing the shallow invaginated cavity forward to the median plate. The enclosed cavity opens by the median slit between the two flaps; anteriorly it is open along the line where sternite XIV abuts against the median plate of XIII. In impregnated females this cavity is filled with a large mass of clear sperm-free material which seals up the openings. In *Xiphopeneus* and, as it appears from figures of the external surface, in section 2 of division 1 of *Trachypeneus* the lip of the groove does not recede from the median plate, and the lip is not produced into two lateral flaps. In *Parapeneopsis*, and from figures of the external surface, apparently in division 2 of *Trachypeneus*, the median portion of the groove is not present, and a cavity is formed between raised lips of XIV and the median plate only laterally. It is a curious fact that in some species of *Parapeneopsis* a copious sperm-free mass is poured out by the males over the surface of the thelycum, in a quantity much more massive than is necessary to seal the narrow lateral openings of the sperm receptacles. This mass is clearly homologous to that enclosed in the unpaired pocket of division 1 of *Trachypeneus* and of *Xiphopeneus*.

In adult females of *T. similis*, those portions of the transverse groove that embrace the lateral posterior margins of the median plate become deeply invaginated to form a pair of large three-lobed membranous sacs, the main lobes of which extend back dorsad the unpaired pocket nearly to the posterior margin of the pereion. A smaller lobe projects anteromedially for some distance dorsad the median plate on each side and another anterolaterally, dorsad the lateral lip of the groove. In impregnated females these membranous sacs are completely filled with a copious semiliquid body of free spermatozoa. The groove is sealed with the yellow secretion filling the unpaired pocket, except at its most anterior point on either side. It is at this anterior gap, apparently, that the sperm, which are probably introduced into the sacs by way of the posterior median part of the groove, find an exit. In *Xiphopeneus* the sperm sacs are much like those of *Trachypeneus similis*, and it is probable that this is also true of the remaining species of *Trachypeneus*. In *Parapeneopsis* the pair of invaginated sacs are not present, and the sperm receptacles consist only of the minute space between the lip of the groove, which is present only anterolaterally, and the posterolateral margins of the median plate. In the second genus (*Metapeneus*) related to *Trachypeneus* which has been included in *Penaeopsis*, and apparently in the first genus and in *Atypopeneus*, the sperm cavity is essentially like that of *Parapeneopsis* or an immature female of *Trachypeneus similis*, and consists of the uninvaginated groove between a lip of sternite XIV and the

median plate which the lip embraces. In these three genera, the lip is obliterated for a short stretch posteromedially, so that the receptacles are separated, as a pair of extremely elongate lateral cavities whose posterior entrances and anterior exits are much more remote from one another than in *Trachypeneus*, most species of *Parapeneopsis*, and *Xiphopeneus*. The internal structure of the thelycum of *Trachypeneus constrictus* has been described and figured by Andrews, 1911, but without any clear indications of its nature and homologies. The thelycum of *T. curvirostris* and of several species of the *Trachypeneus* series has been somewhat obscurely discussed by Kishinouye, 1900.

The *Trachypeneus* type of thelycum is perhaps homologous to that of the species of *Penaeus* with enclosed sperm cavity, in which, however, the lips of the groove of XIII arise far posterior to the posterior margin of the median plate, so that a single unpaired cavity like the median pocket of *Trachypeneus* is formed, but within which the sperm mass and not a sperm-free male secretion, is stored. In the thelycum of *Penaeus* the anterolateral lips of the groove barely lap the median plate, and therefore define only the exit slits of the undivided sperm receptacles, not the receptacles themselves as in the *Trachypeneus* series.

The intermediate portion of the vas deferens of the male of *T. similis* contains sperm enclosed, 150 to 200 each, in minute spherical sacs whose walls break very easily. The spermatozoa are shaped like swollen bi-convex disks, from the middle of one face of which a short point projects. The sperm are elaborated into packets in the complexly coiled upper vas. The intermediate portion of the vas is a simple tube without the typhlosole-like invaginations of its wall found in *Penaeus*. At the lower end of the vas a larger glandular mass is present which appears to secrete the clear yellow material stored in the unpaired pocket of the female.

The petasma of the male is quite different from the simple open pod-like appendage of *Penaeus*. Those portions equivalent to the lateral margins in *Penaeus* are folded mediad across the posterior face of each ramus, while the distolateral corners are greatly produced as spoutlike horns open along their distal margins. The posterior walls of the spouts are produced in adults and lap over the anterior walls, thus producing an incompletely sealed tube with a subterminal opening. The petasma of all genera of the *Trachypeneus* series seems to be of this general form. In some species of *Parapeneopsis* the tube is completely sealed by fusion of its anterior and posterior lips, forming a perfected injection apparatus. In the second genus (*Metapeneus*) previously included in *Penaeopsis*, the horns are quite short and broadly open, although the anterior wall

may be produced as a large flap lapping over the posterior wall. A probably homologous pair of lateral horns are found in Eusicyoninae and in *Artemesia* in which, however, the channeling is very shallow. In the possession of a pair of posterior spines in addition to the lateral ones, the petasma of Sicyoninae resembles that of the *Parapenaeus* series, and thus seems to approximate this more than the *Trachypeneus* series of Penaeinae.

It is possible that the numerous spermatophores are poured out of the genital apertures and placed in the petasma, as are the pair of large spermatophores in *Penaeus*, but the difficulty of handling a loose mass of minute bodies in this manner leads me to believe that the lower parts of the vasa deferentia are everted and laid within the proximal portion of the petasma as hose is coupled to a nozzle. The points of the lateral horns are probably inserted through the T-shaped opening posterior to the median plate into the orifices of the lateral invaginated sacs until the transfer of spermatophores is completed, then partly withdrawn to effect an injection of the sperm-free mass into the unpaired pocket.

RELATIONSHIP TO OTHER SPECIES.—From its description until the present, *T. similis* has been incorrectly regarded as no more than a varietal form of *T. constrictus*, except by Rathbun, 1901, whose statement of the differences between the species does not include the more dependable diagnostic characters. Of the differential characters that have been pointed out by previous workers, the pubescence of the branchial region of the carapace and posterior pleonic somites is subject to considerable variation. In any locality, *T. similis* is more pubescent than *T. constrictus*, but the latter is never completely naked and glossy. Louisiana specimens of *T. constrictus* are more pubescent in the posterior part of the branchial region and the sides of the sixth pleonic somite than are many specimens of *T. similis* from the West Indies. The length of the terminal portion of the telson and of the posterior pair of mobile lateral spinules is also rather variable; again, specimens of the two species from any one locality are readily differentiated; but the point of the telson and the lateral spines are in Louisiana specimens of *T. similis* considerably shorter and stouter than in Puerto Rican material, and almost as short as in *T. constrictus* from the northern Atlantic coast of the United States.

The postrostral carina seems generally to fade away posteriorly in *T. constrictus* more than in *T. similis*; but this structure and the rostra of the two species present no diagnostic characters. The antennal peduncle is in *T. similis* usually much longer and slenderer than in *T.*

*constrictus*, and always extends well beyond the tip of the external scale of the antennular peduncle, but it is occasionally almost as short as in *T. constrictus*.

The most reliable diagnostic characters, which are provided by the sculpture of the male and female genital sterna, have not been previously described. In adult females of *T. constrictus*, the anterior margins of the median plate and the lips of the transverse groove of the thelycum are convexly rounded, whereas in *T. similis* they are truncated, there is a median notch in the anterior margin of the median plate, and the lateral flaps of XIV have the anterior margins to some extent concave. The lateral flaps overlap the elevated median plate in *T. constrictus*; they may occasionally do so to a slight extent in *T. similis*. The median separation of the lateral flaps usually extends farther back in *T. similis* than in *T. constrictus*. The rib that supports the expanded median plate and extends anterior to it is always sharply set off from the anterior ventral margin of the plate in *T. constrictus*, but it is sometimes so set off in *T. similis*. The ventral surfaces of the thelycum of *T. constrictus* seem always to be pubescent; those of *T. similis* naked. The thelycum of *T. constrictus* has been figured by Milne-Edwards and Bouvier, 1909.

In the male of *T. similis* the sternal elevation lying between the bases of the fifth legs always presents lateral margins sloping regularly to the narrow posterior end; whereas in *T. constrictus* the margins are always somewhat indented to set off the posterior part of the plate from its broad anterior basal portion. The sculpture of the male fourteenth sternite of *T. constrictus* has been fairly well figured by Milne-Edwards and Bouvier.

The exopodite of the fifth leg of *T. constrictus* is larger and longer than in *T. similis*, in which it never reaches so far as the distal end of the basis. The base of the terminal point of the telson is always enlarged into a broad shoulder from which the slenderer distal part is well set off; whereas the tip usually tapers regularly to a point in *T. similis*; however, some indication of a proximal shoulder is occasionally present in *T. similis*.

In both of the species of section 1 of the subgenus there is an unfilamentose vestige of an anterior arthrobranch on somite XIII which, although present in the Pacific American species of section 2, seems to be absent in *T. curvirostris* and has not been noted heretofore as occurring in the genus. The longitudinal sutures of both species of section 1 extend beyond the middle of the carapace but not to the level of the transverse, which is present in both species although wrongly stated by Milne-Edwards and Bouvier to be absent in *T. constrictus*. The antero-inferior angle of the carapace is always truncated and is not produced

into a pterygostomian spine, such as is described and figured by Milne-Edwards and Bouvier, 1909. There are four pairs of mobile spines on the lateral margins of the telson, of which only the distalmost is conspicuous. The petasma of the two species is quite similar and closely resembles that of *T. curvirostris*. It is usually somewhat shorter and broader, with more proximally and posteriorly curved lateral horns in *T. similis* than in *T. constrictus*. The antennular flagella are considerably shorter than the carapace and can hardly be described, as in the key offered by Hay and Shore, 1918, as moderately long in comparison to those of *Parapenaeus longirostris*.

The color in life of *T. constrictus*, from Beaufort, North Carolina, has been described by Hay and Shore as translucent white with purplish-gray cloudings and blotches and pinkish appendages; and Verrill, 1922, describes specimens from Bermuda in fairly similar terms. The color in life of specimens of *T. similis*, taken in 15 fathoms off Pass à la Loutre, Louisiana, was as follows: eyes green; body mottled with orange-red; walking legs and pleopods orange-red with opaque white patches; uropods deep red with a white margin.

### **Trachypeneus constrictus** Stimpson

*Penaeus constrictus* STIMPSON, 1871.

*Parapenaeus constrictus* SMITH, 1886.

*Penaeopsis agassizi* BOUVIER, 1905.

*Trachypeneus constrictus* ALCOCK, 1906.

Not *Trachypeneus constrictus* CARY AND SPAULDING, 1909.

One female was taken off Timbalier Island; two to eastward, off Pass à la Loutre. The largest female had a carapace length of 12.5 mm., as compared with 20 mm. for the largest of *T. similis*.

### **XIPHOPENEUS** Smith

The genus is confined to America. It is distinguishable from *Trachypeneus* by the multiarticulate dactyls of the last two pairs of thoracic legs, the long antennular flagella, and the absence from the carapace of the adult of a transverse suture; Alcock, 1906, has erroneously stated that the transverse suture is present. This structure is, however, present in three preadults of *X. riveti* Bouvier, about 25 mm. in length (kindly loaned for examination by the Peabody Museum of Natural History) and it is faintly indicated in somewhat larger individuals of *X. kroyeri*. The rostrum loses its distinctive styliform appearance in the preadults, and is quite similar to that of *Trachypeneus*; while the

number of joints of the dactyls is reduced. An additional difference between *Xiphopeneus* and *Trachypeneus* is supplied by the telson, which is completely unarmed in the former. The basis of the external maxillipeds is unarmed; the basis and the ischium of the first legs only, armed. The first pleopod of the female lacks a rudimentary endopod such as is perceptible in *Trachypeneus similis* and many other Penaeidae. *Xiphopeneus* resembles section 2 of division 1 of *Trachypeneus* in the single, transverse opening of the unpaired pocket of its thelycum.

### ***Xiphopeneus kroyeri* (Heller)**

#### Figure 12

*Peneus kroyeri* HELLER, 1862; MIERS, 1878.

*Xiphopeneus harttii* SMITH, 1871.

*Xiphopeneus kroyeri* SMITH, 1886.

DISTRIBUTION.—*Xiphopeneus kroyeri* has been recorded from Louisiana, Puerto Rico, and Brazil. A Pacific-American congener, *X. riveti* Bouvier, has been described from Peru. I have examined an extensive series of specimens from Louisiana, and four males from the west coast of Panama in the collection of The American Museum of Natural History; also two females from Bahia, Brazil, that appear to be cotypes of Smith's *X. harttii*; and three preadult individuals from Acajutla, El Salvador, in the collection of the Peabody Museum of Natural History at Yale. All this material seems to be specifically indistinguishable, although some differences probably indicating local differentiation are perceptible.<sup>1</sup>

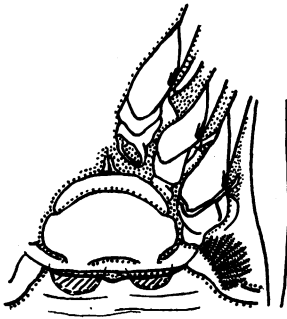
STRUCTURE AND NATURAL HISTORY.—*Xiphopeneus* occurs in sufficient abundance along the entire Louisiana coast to be of some importance to the commercial drying-platforms. It seems rarely to enter the inside waters, and has not been taken in the insufficiently explored outer littoral zone.

The internal structure of the thelycum differs only in details from that of *Trachypeneus similis*; while in the unproduced median lips of the unpaired pocket, *Xiphopeneus* seems to resemble closely *T. curvirostris*. The bilobed pair of invaginated saclike sperm receptacles are relatively larger than in *T. similis*, and the main lobes may extend back into the first pleonic somite. The anteromedian lobes present in *T. similis* are absent in *X. kroyeri*. It is quite usual to find one saclike receptacle more completely filled with spermatophores than the other; and occasionally

<sup>1</sup>Recent accessions to the Bingham Oceanographic Collection include two new records of *Xiphopeneus kroyeri*: one from the Atlantic coast of the United States, off St. Augustine, Florida; the other from the Caribbean coast of Panama, in Limon Bay.

one sac is completely empty. The sperm are of different shape from those of *T. similis*, the elongate pear-shaped head tapering gently into the conical point. The walls of the minute spermatophores are more resistant than in *T. similis*, and the packets persist after deposition in the receptacles, a characteristic which is also true (Kishinouye, 1900) of *T. curvirostris*.

The **p**etasma is similar in character to that of *Trachypeneus*, and probably functions in the same way. The upper portion of the vas deferens is extremely long, much coiled, and differentiated into several sections. The slender tubule leading from the testis contains free spermatozoa; the enlarged more distal tube contains clumped masses of sperm not yet enclosed in a retaining membrane. The large tube narrows, then enlarges to merge into the intermediate portion of the vas deferens, which is filled with completed spermatophores. At the juncture of these two sections is a glandular evagination which appears to secrete the material of the envelope. Just behind the genital aperture, the vas gives off a large, evaginated pouch which appears to secrete and store the copious yellow material which fills the ventral cavity of the thelycum. The male genital apertures are conspicuously



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Fig. 12. *Xiphopenaeus kroyeri* (Heller).

Thelycum, with filled sperm sacs showing through pleonic integument.

The male genital apertures are conspicuously "sub-coxal."

**VARIATION WITHIN THE SPECIES.**—Bouvier has noted as specifically distinctive of his two Peruvian females of *Xiphopenaeus* certain characters in which his material does not agree with the description of *X. kroyeri* by Smith. I find that certain of these distinctions have no actual basis, Smith's description not coinciding with Brazilian material in these respects, and the characters mentioned by Bouvier being common to the genus. In other supposedly diagnostic characters, Bouvier's specimens do not appear to have been typical, a circumstance perhaps correlated with their very great size.

In *Xiphopenaeus* from Louisiana, although there is considerable individual variation in length of rostrum, the ratio of rostral to carapace length is correlated with change in the latter. In individuals of carapace length less than 9 mm., the rostrum is shorter than the carapace. Above 9 mm., rostral length increases more rapidly than that of the carapace,



and the rostrum becomes considerably longer than the latter. At the largest size (above 24 mm. for females and 21 mm. for males) the rostrum is once more reduced in proportion to carapace, although still slightly longer than the latter. The rostrum is somewhat longer in females than in males. The Brazilian females were near the Louisiana series in rostral length. The larger specimen was above the maximum size for the latter material, the carapace length measuring 31 mm. The rostrum of this female was 31.5 mm. in length. The four males from Pacific Panama average above 22 mm. in carapace length, a greater size than the maximum in Louisiana males. The rostrum averages over 4 mm. longer than the carapace, a greater length than is found in any Louisiana specimens of either sex. Bouvier, 1907, describes the rostrum of his Peruvian specimens as shorter than the carapace, a condition at variance with my finding of a longer rostrum than in Atlantic material in Panama specimens; but Bouvier's specimens were much larger than any others recorded for the genus. I believe it probable that a series of rostral changes comparable to those occurring in the Atlantic form occur in the Pacific stock, but that the latter is of larger size than the former at any given rostrum-carapace ratio.

The short rostrum of the Peruvian specimens therefore probably represents a reduction correlated with the attainment of great size and is almost certainly not to be considered as a character distinguishing a Pacific from an Atlantic species.

*X. riveti* was described as with four conspicuous rostral teeth and a fifth rudimentary anterior one. Of 27 Louisiana specimens examined, 2 had six, 16 had five, and 9 had four rostral teeth. The anterior tooth was either large or completely absent. In Panama specimens there were five teeth, of which the anterior was not reduced.

The anterior cervical sulcus never reaches the anterior margin of the carapace as in Smith's figure.

The small tooth at the posterior end of the dorsal carina of the fourth pleonic somite, not described by Smith, is present in the Brazilian specimens, although perhaps slightly smaller than in Louisiana and Panama material.

The height of the rostral crest seems somewhat variable in material from all localities; it is always somewhat less high, and with the teeth of the crest less crowded than in Smith's figure. The styliiform part of the rostrum is always elevated relative to the distal portion, but the latter may be sufficiently depressed to bring the former to the horizontal.

The length of the inferior antennular flagella is described by Smith

as one-half that of the superior; that of *X. riveti* by Bouvier as one-fourth. In Louisiana and Panama specimens the length varies from two-ninths to two-fifths, the variation not being correlated with size or sex, and apparently not caused by breakage. The flagella of the Brazilian specimens available to me were broken. In Louisiana and Panama material, the superior ramus of the antennule is not much more than two and one-third times the length of the carapace, instead of being more than three times as long, as described by Smith. The antennal scale extends well beyond the tip of the antennular peduncle instead of only to the base of the flagella, as it is described by Heller as well as by Smith. The exopodites of the two posterior pairs of maxillipeds are, as described for *X. riveti* by Bouvier, quite broad rather than very slender in material from all localities. The cutting edge of the mandibles, although individually somewhat variable, seems about the same in material from all localities.

The petasma as it occurs in Louisiana and Panama males is almost identical, although the small tooth on the posterior face of the lateral cornua near the base is more conspicuous in the latter. The petasma of Brazilian males is probably not very well represented by Smith's figure. The thelycum of Peruvian specimens is, as described in very general terms by Bouvier, not differentiable from that of Louisiana and Brazilian material. The thelycum of the latter is perhaps slightly shorter and wider than that of Louisiana specimens.<sup>1</sup>

The maximum size of the Pacific stock and apparently of that from Brazil is greater than that from Louisiana. The epigastric tooth is set relatively slightly closer to the orbital margin in specimens from Brazil than in those from Louisiana, and slightly closer in the latter than in Panama specimens. The adrostral carinae extend somewhat farther back in specimens from Panama than in those from Louisiana, and in the latter than in Brazilian specimens. The depressions in front of the hepatic spine and the anterior cervical sulcus are more heavily pubescent, and the distal portion of the rostrum is deeper in Panama specimens than in those from the Atlantic. The walking legs are perhaps somewhat longer in Brazilian than in Pacific forms, and in Pacific than in Louisiana material, but great individual variation makes this a difficult point to ascertain without more material from the former localities.

The form of *Xiphopeneus* found in the Gulf of Panama seems to be hardly more differentiated from the Atlantic stock than are Brazilian and Louisianian forms from one another. Therefore, unless the Peruvian

<sup>1</sup>The thelycum of Pacific females from the Gulf of Panama, collected during a recent expedition of the Bingham Oceanographic Foundation, displayed no clear differences from Louisiana material.

is distinct from Panamanian stock, I am inclined to regard *X. riveti* Bouvier as a varietal form of the single species of the genus, *X. kroyeri* (Heller).

#### PARAPENAEUS Smith

The exact delimitation of the genus has been a matter of some difficulty since its first definition by Smith, 1886. In particular, the boundary between *Parapenaeus* and the three genera, two of which are trachypeneine, heretofore confused under the names *Penaeopsis* Bate or *Metapenaeus* Wood-Mason and Alcock has been obscure. I find that *Parapenaeus* may be described as follows: a spine on the ventromedian margin of the basal segment of the antennular peduncle persistent in the adult; first chelipeds with a spine on basis and ischium, the others unarmed; a pleurobranch and a posterior arthrobranch, no vestigial anterior arthrobranch on somite XIII; exopodites well developed on the posterior two pairs of maxillipeds, minute but present on the walking legs; a distal pair of fixed lateral teeth on the telson preceded by a pair of minute mobile spines; a branchiostegal or true pterygostomial tooth (as contrasted with a merely produced anteroinferior angle) on the carapace, except in *P. longipes*; thelycum with a pair of invaginated sperm receptacles, but without median pocket; sperm mass not organized into numerous minute spermatophores; petasma usually with two pairs of distal spines, posterior and lateral, in addition to the anteromedian distal lobes (the distolateral spines and the lamellae at their bases not forming a deeply channeled spoutlike injection apparatus); longitudinal and transverse sutures present on the carapace; rudimentary arthrobranch of VII without filaments.

Of these characters only the last two clearly distinguish *Parapenaeus* from one of the genera included under *Penaeopsis*. Some of the species of this third genus of "*Penaeopsis*" have an open unarmed petasma, while the rest have an asymmetrical petasma modified from the *Parapenaeus* type. The former group lacks, the latter usually possesses, the vestigial arthrobranch of XIII absent in *Parapenaeus*. Some species of both groups of this genus of "*Penaeopsis*" have a basal spine on the second legs. Both groups have more than one pair of mobile lateral spines proximad the fixed pair of the telson.

Schmitt, 1926a, has proposed an insufficient definition of *Parapenaeus* and in the same paper has tentatively placed *Parapenaeus paradoxus* Bouvier in *Penaeopsis*. Since Bouvier's species is not only synonymous with *Parapenaeus politus* Smith, but with *P. longirostris* (Lucas), this

action is equivalent to removing the type species from the genus. Schmitt suggests that should *P. paradoxus* actually be a *Parapenaeus*, the definition of the genus must be modified to allow for the presence of exopodites "on the first legs." I find that small exopodites are present on the first three legs of *Parapenaeus longirostris*, as described by Milne-Edwards and Bouvier for *P. paradoxus*, and that minute vestiges occur on the last two pairs of pereopods in large specimens. Similar small exopodites are probably also present in the other species of the genus, in which their occurrence has been denied. Schmitt's statement that "the telson (of *Parapenaeus*) is without movable spines," although in accord with previous descriptions, is incorrect. The emphasis which his definition places on the absence of a vestigial anterior arthrobranch from somite XIII of *Parapenaeus* is misleading, since in several species of *Penaeopsis* this structure is also absent. Schmitt's appended suggestions for a subdivision of *Penaeopsis* are not in accord with the natural boundaries of the three genera confused under this title, and obscure the close relationship of one of these genera to *Parapenaeus*.

*Artemesia* Bate, which has been inaccurately described, and which has occupied an anomalous position, agrees very closely in structure with the *Parapenaeus* series. It will be considered in detail in a forthcoming paper.

The species of *Parapenaeus*, according to the present definition, are five in number: *Parapenaeus longirostris* (Lucas) and *P. americanus* Rathbun in the Atlantic; *P. fissurus* (Bate), *P. investigatoris* Alcock and Anderson, and *P. longipes* Alcock in the Indo-Pacific.

According to De Man, 1911, the Indo-Pacific species of *Parapenaeus* lack epipodites on the third legs, but Balss, 1914, finds epipodites to be sometimes present in *P. fissurus*. They are absent in the two specimens of *P. americanus* that I have examined. In *P. longirostris* (*P. paradoxus*), according to Milne-Edwards and Bouvier, the epipodites may be occasionally lacking. I have found them absent in one small specimen from the Louisiana coast.

#### ***Parapenaeus longirostris* (Lucas)**

*Peneus longirostris* LUCAS, 1849.

*Penaeus membranaceus* HELLER, 1862.

*Penaeus bocagei* JOHNSON, 1863.

*Parapenaeus longirostris* SMITH, 1886.

*Penaeus politus* SMITH, 1881.

*Parapenaeus politus* SMITH, 1886.

*Neopenaeopsis paradoxus* BOUVIER, 1905.

*Parapenaeus paradoxus* MILNE-EDWARDS AND BOUVIER, 1909.

*Penaeopsis paradoxus* SCHMITT, 1926a.

Not *Parapenaeus paradoxus* BOONE, 1927.

DISTRIBUTION.—*P. longirostris* occurs in the Mediterranean and eastern North Atlantic ("*P. longirostris*"); on the Atlantic coast of the United States as far north as Martha's Vineyard ("*P. politus*"); along the northern shore of the Gulf of Mexico, from which there appears to be no previous published record; the southern shore of the Gulf of Mexico ("*P. paradoxus*") and the Gulf of Paria ("*P. politus*"). It is the only American penaeine that also occurs on the coasts of Europe, although *Penaeus brasiliensis* ranges to the African coast. No Pacific American congener has been reported.

STRUCTURE AND NATURAL HISTORY.—The largest female taken was about 100 mm. in total length; the largest male, 65 mm. Twenty-five females and ten males were taken at a single locality in the inner littoral zone, about five miles off Pass à la Loutre, in a depth of 15 fathoms, during later winter and spring. I think it probable that the species is more abundant farther offshore, and that large adults only rarely penetrate the inner littoral.

The thelycum is essentially of the same type as in the *Trachypeneus* series, and consists of a transverse groove on the anterior part of somite XIV, the posterior lip of which embraces the posterior and posterolateral margins of the median plate of XIII. The lateral portions of the groove are deeply invaginated to form a pair of large membranous sperm receptacles, running back beneath the integument of XIV. The median portion of the groove is shallow and is filled with a clear sperm-free material in impregnated females. A short shallow median longitudinal groove runs back from the transverse groove. The sides of sternite XIV are raised as broad ridges which are continuous anteriorly with the enlarged lateral portions of the lips of the transverse groove. These lateral portions lap over the posterolateral parts of the median plate, hooding the openings of the sperm sacs. It appears to me that the amorphous masses of sperm are both introduced into and withdrawn from the sperm sac of each side by the same slitlike opening, which is not separated into an anterior exit and posterior entrance as in the *Trachypeneus* series.

This thelycum is almost completely identical with that of those members of the third genus confused under the name *Penaeopsis* which have a simple podlike petasma. The remaining species of this third genus, with an asymmetrical petasma clearly derived from the type found in *Parapenaeus*, lack the greatly enlarged membranous invagina-

tions of the transverse groove. *Eusicyonia* has a thelcyum that closely resembles that of *Parapenaeus*.

The vas deferens of the male is internally partitioned by a typhlosol-like evagination of its wall, as in *Penaeus*. The lower end of the vas is enlarged, and part of its wall is hypertrophied as a whitish mass of glandular tissue that partly surrounds a pear-shaped mass of sperm-free secretion. The lower part of the enlarged end of the vas is filled with a mass of sperm in a gelatinous matrix, surrounded by a very thin envelope. The spermatozoa are shaped much as in *Penaeus*. The pear-shaped mass of secretion, contrary to the view expressed by Heldt, 1932, appears to be transferred to the female, and to function in sealing the entrances to the sperm cavities.

The petasma of *Parapenaeus longirostris* resembles that of the *Trachypeneus* series in that it is not open, the parts that form the lateral margins of an open petasma being folded across the posterior faces of the endopods nearly to the midline. The anteromedian lobe of the distal margin of each of the petasmas endopods is greatly produced as an extremely long curved spine. At the lateral corner of the distal margin of each endopod is a stout spine; and a similar spine springs from the posterior distal margin. At the inner bases of these spines a complexly folded and produced continuous membranous flap originates, which closes in the distal opening of the space between the anterior and posterior faces of the petasma.

This petasma differs essentially from that of the *Trachypeneus* series in that a posterodistal spine is present on each half of the petasma, and in that the lamellae at the base of the laterodistal spine, probably homologous to the lateral cornua of the *Trachypeneus* series, are not produced as a spoutlike channel for the conduction of sperm. The petasma of *Parapenaeus longirostris* seems to be represented in modified form in one group of the third genus that has been included under *Penaeopsis*; while the other group has a simple podlike petasma resembling that of the *Penaeus* series, *Aristaeinae*, and *Solenocerinae*. The petasma of *Artemesia* Bate differs from that of *Parapenaeus* in that the flaps springing from the bases of the laterodistal spines are produced as rigid, shallowly channeled cornua resembling those of the *Trachypeneus* series. The petasma of *Eusicyonia* is of the same essential type as that of *Parapenaeus longirostris*, but the laterodistal spines are shallowly channeled, the membranous flaps often present in *Parapenaeus* appearing to be fused with them. From the figures by Alcock, 1906, it appears that the laterodistal spines of *Parapenaeus* may sometimes similarly be channeled;

the posterior spines much reduced; the anteromedian projections not hypertrophied as spiniform projections; or the membranous flaps reduced to slight processes of the distal margin of the petasma.

VARIATION WITHIN THE SPECIES AND RELATIONSHIPS TO OTHERS.—In addition to the Louisiana material, several Venezuelan specimens and a Mediterranean female of *P. longirostris*, in the collection of The American Museum of Natural History, I have been enabled, through the kindness of the Museum of Comparative Zoölogy, the Peabody Museum of Natural History, and the U. S. National Museum, to examine a female from Martha's Vineyard and a number of specimens from the Gulf of Paria identified as *P. politus* by S. I. Smith; four Mediterranean males and females; cotypes of *P. paradoxus* Bouvier from north of Yucatan; and a number of specimens from off Cape Hatteras and Beaufort on the Atlantic coast of the United States and from the Gulf of Mexico off western Florida. I am unable to discover any seemingly significant differences between any of these specimens.

Smith, 1886, distinguishes *P. politus* from *P. longirostris* by differences in the rostrum, with the remark that a larger series of specimens might show it to be only a variety of *P. longirostris*. Bouvier characterizes *P. paradoxus* as with a shorter rostrum than the European form. The rostrum of large European specimens, which attain a maximum size far above that recorded for American material, reaches beyond the middle of the second segment of the antennular peduncle in the male, and even exceeds the antennal scale in very large females. It displays a more or less marked sigmoid curve with base and tip ascending. The anterior portion is unarmed, while the proximal dorsal margin bears usually seven teeth in advance of the epigastric. Typical *politus* has a rostrum never much exceeding the base of the second segment of the antennular peduncle, armed almost to the tip usually with seven teeth in advance of the epigastric. The tip is depressed. *Politus* from Venezuela may have a longer rostrum, as was noted by Smith. *Paradoxus*, although this comparison is not made by Bouvier, has a rostrum identical with that of *politus*.

In Louisiana females, the rostrum varies from a condition identical with that in *politus* to a very long rostrum agreeing perfectly with that found in *longirostris*. An examination of the series reveals that the depressed *politus* rostrum, armed almost to its tip, corresponds to the proximal two flexures of the *longirostris* rostrum, and that the development of the unarmed reascending distal portion such as is characteristic of *longirostris*, although subject to individual variation, is conditional on

size. The smallest Louisiana females have the *politus* rostrum, while larger females usually display some length of horizontal unarmed tip. Above 90 mm. the rostrum generally has an ascending styliform tip that completes the sigmoid curve, and may extend well beyond the antennal scale, precisely as in large European females. No specimens that have been identified as *P. politus* and *P. paradoxus* appear to have been as large as the Louisiana females with complete *longirostris* rostrum. Bouvier, 1908, has noted that in European material, apparently adult but of mediocre size (about 80 mm.), the rostrum does not extend beyond the middle of the second article of the antennular peduncle. Therefore, it seems probable that a typical *politus* rostrum may be found to occur in European as well as American specimens, of appropriate size. All males from Gulf and Caribbean localities that I have examined possess a very short *politus* rostrum hardly exceeding the eyes. However, the largest of these specimens is not over 65 mm. in length, while the *longirostris* male described from the eastern Atlantic by Bouvier, 1908, was 80 mm. in length, and the smaller Mediterranean male that I examined was 90 mm. in length. This disparity in size appears sufficient to account for the fact that no available western Atlantic males have a rostrum so elongate as that of described European males.

It thus appears that described differences in rostrum are not sufficient even for the establishment of varietal distinctions, and are merely based on different stages in the origination and increase in length of the styliform distal part of the rostrum, all of which may occur in the growth of a single individual. It is probable that in some western localities the species does not attain a size so great and a rostrum so elongate as that of eastern Atlantic and Mediterranean specimens; and also that the same rostral condition is not correlated with the same size in all localities; but, as noted for *Penaeus setiferus*, there is no reason for believing that such differences imply hereditary racial distinction.

Some variation in the position of the epigastric tooth is portrayed in the literature. Thus, Bouvier, 1908, figures the epigastric of *P. longirostris* as placed in front of the level of the hepatic tooth, as does Heller, 1862; while Milne-Edwards and Bouvier, 1909, figure the epigastric of *P. paradoxus* as behind the hepatic. In the description of *Penaeus bocagei* by Brito Capello, 1864, and in the figure of *P. longirostris* published by Boone, 1930, the epigastric is placed posterior to the hepatic, which position it occupies in all material that I have seen.

I note some differences not described in the literature in the depth of the depression that accompanies the longitudinal suture. This de-



pression is comparatively deep in the Mediterranean specimens and the Martha's Vineyard female. In the Yucatan and Venezuelan material it is shallower, while in specimens from Florida and Louisiana it is hardly perceptible. The depression seems somewhat deeper in males than in females from all localities. These differences, if they have any significance whatever, are certainly not correlated with previously accepted taxonomic distinctions. There is also some variation not clearly correlated with locality in the length and distance from the margin of the branchiostegal spine, which is perhaps placed closer to the margin in small than in large specimens.

Milne-Edwards and Bouvier state that the sixth pleonic somite is longer in *P. paradoxus* than in *P. longirostris*. I find this segment to be of about the same length in specimens of the same size from all localities. There is, however, a distinct decrease in proportional length with increasing size; thus, in a graded series of Louisiana specimens ranging from 7 to 20 mm. in carapace length, the length of the sixth pleonic segment in proportion to the carapace decreased regularly ten per cent from smallest to largest. A comparison of the specimens representing *P. paradoxus*, all small, with larger European individuals is thus perhaps the basis of the supposed difference between the two.

The thelycum of material from all localities is very similar. Slight differences between European and American material in relative size of median plate and in shape of the lateral ridges of sternite XIV are visible, but these differences seem insufficiently constant to warrant varietal separation of the western form until a considerable series of equivalent sizes has been compared.

Bouvier's drawing of the thelycum of *P. paradoxus* differs considerably from that of Senna, 1903, of the same structure in Mediterranean specimens, the latter being a crude but recognizable representation of the organ as found by me in all American materials. A careful comparison of the two figures, using the position of the base of the fifth leg as an orientation mark, shows that Bouvier may have placed the posterior margin of the thelycum considerably anteriorad the position in which it actually occurs, thus excluding from his figure the entire posterior portion of the organ. The paired internal sperm sacs of *Parapenaeus*, when filled with the opaque sperm mass, may be seen through the translucent integument. The posterior margins of these sacs lie in approximately the position in which Bouvier's drawing shows the posterior margin of the thelycum; and it is probable that Milne-Edwards and Bouvier have

mistakenly attributed the margin of the internal structure to the sternal plate lying above it.

The eyes of *P. politus* are mentioned by Smith, and those of *P. paradoxus* are described by Milne-Edwards and Bouvier as being more reduced than those of *P. longirostris*. I am unable to detect any distinctions between material from the various localities in the proportionate dimensions of these organs other than those induced by shrinkage.

Hay and Shore, 1918, have characterized *P. politus* as with "antennular flagella short" in comparison with those of *Trachypeneus constrictus*. The flagella are properly to be considered as long, those of the female equaling or even exceeding the length of the carapace, while those of the male sometimes exceed even the carapace plus the rostrum.

Milne-Edwards and Bouvier state that the palp of the second maxilla of *P. paradoxus* has the armature of its tip "reduced" to two spines. In Louisiana material an external view of the palp, such as is given in Bouvier's figure, reveals two spines, only one of which, however, is placed on the external surface. The other, which is visible above the margin in the position indicated by Bouvier, is borne on the internal surface. The internal surface further bears a variable number of similar spines, usually seven or eight, invisible in an external view. I doubt that a reduction in armature in *P. paradoxus* actually exists.

The tip of the mandibular palp of *P. paradoxus* is described and figured by Milne-Edwards and Bouvier as rounded, while that of *P. longirostris* is described by Bouvier as truncate. In Louisiana material the tip of the palp is clearly truncated in the larger specimens, but the sharpness of the cut is lost with decreasing size, until in small specimens the tip could be described as rounded.

Milne-Edwards and Bouvier believe that *P. paradoxus* is probably closely related to *P. politus*, but state that descriptions of the latter are not complete enough to permit a formulation of the differences. From this statement, it seems evident that *P. paradoxus* was regarded as sufficiently characterized by the presence of exopodites, supposed to be lacking in other members of the genus, on the thoracic legs of some specimens. The vial of "*P. paradoxus*" from Yucatan that I examined contained the label "Ex. depourvu d'exopodites sur les pattes mais avec un epipodite sur p. 3." These examples, nevertheless, proved to have inconspicuous appendages in the position where exopodites appear in other penaeids. Specimens from other localities were all possessed of similar appendages that varied in length up to a fairly conspicuous and unmistakable free exopod half a millimeter long, unsegmented, fleshy, and

tipped with setae of a length not quite equal to its own. These exopods appear to increase in relative length with increase in size of the individual, an occurrence in accord with the fact that in postmysis larvae of *Parapenaeus*, as in other Penaeinae, the exopodites of the pereopods are completely absent, and are only recovered very late in development. Milne-Edwards and Bouvier's statement that exopodites are never present on the fourth and fifth legs of *P. "paradoxus"* is not completely accurate, since traces of exopodites occur on these legs, although they are here reduced to hardly apparent fixed lobules.

In the specimens of *P. "paradoxus"* that I examined, the blade of the epipodite of the third legs was shorter and narrower than in the majority of Louisiana specimens, but in small individuals from the latter locality, as great or a greater degree of reduction in both length and breadth was sometimes observable, while in one specimen with carapace length of less than 12 mm. this pair of epipodites was completely absent. Individual variation in the occurrence of the third epipods will probably be found in all species of *Parapenaeus*.

The petasma, allowing for deficiencies in the drawings, is approximately as it is figured in "*P. longirostris*" by Bate, 1881, and Senna, 1903, and is quite uniform save for slight variation in the length and curvature of the distomedial spines and in the relative proportions of the membranous distal lobes in all material examined.

The color of European specimens of *P. longirostris* is described by Bouvier, 1908, as whitish, with certain regions tinted with rose. The color in life of Louisiana specimens was eyes green, body and appendages mottled with red pigmented and pale translucent areas, exopod and distal half of the endopod of the uropod deep red.

*Parapenaeus longirostris* is clearly distinguished from *P. americanus* Rathbun, a species recorded from the Caribbean, in that the branchiostegal spine of the former is placed some way behind the anterior margin of the carapace, whereas in the latter an equivalent spine is placed on the margin. It is probable that the modal number of rostral teeth is different, that of the former being seven, that of the latter six, in addition to the epigastric placed far behind the orbital margin. I have examined an immature male of *P. americanus* with a carapace length of 10 mm., from St. Lucia, kindly loaned by the Museum of Comparative Zoölogy, and an individual of carapace length 8 mm. from British Honduras in the Bingham Oceanographic Collection. The hepatic spine of the former, and the epigastric as well, are placed somewhat farther from the anterior margin than in *P. longirostris*. The postrostral carina,

as in *P. longirostris*, extends almost to the posterior margin of the carapace. The spine of the anteroinferior margin of the carapace is placed above the anteroventral angle, not at it as in Rathbun's figure. The epipodite of the third legs is absent, and is probably rarely or never present in this species. The smallest available male of *P. longirostris*, of 9 mm. carapace length, has joined petasmas of adult appearance; while that of the male of *P. americanus* is too immature to permit a determination of its characters. *P. americanus* is certainly closely related to the Indo-Pacific *P. fissurus* Bate, and, for the present, I can name no characters by which it may be distinguished, although such probably exist. *P. americanus* will probably be found to have a congener on the west coast of America.

The Indo-Pacific *P. investigatoris* Alcock and Anderson, which in the position of its branchiostegal spine resembles *P. longirostris*, differs from it by its usually fewer rostral teeth, shorter postrostral carina, usually absent epipod of the third legs, and somewhat different thelycum and petasma. As in *P. fissurus*, the buttress of the anteroinferior tooth of *P. longirostris* is continued as a sharp carina some distance toward the hepatic; but, as in *P. investigatoris*, a shallow sulcus dorsad the tooth and carina continues to the hepatic spine and there turns posteriorly. *P. longipes* Alcock differs markedly from the other species of the genus in the absence of a spine from the anteroinferior region of the carapace.

#### **Eusicyoninae**, new name

Sicyoninae, ORTMANN, 1901.

The subfamily, comprising only the genus *Eusicyonia*, has been regarded as very distinct from the remainder of Penaeidae, and, if resembling any other group, as stated by Milne-Edwards and Bouvier, 1909, to "rapprocher d'avantage des Aristéinés que des Pénéinés." I find that the Eusicyoninae are very closely related to Penaeinae, with which they form a group set off, especially by the developmental history, from Aristaetinae and Solenocerinae. The characters in which Eusicyoninae differ from Penaeinae are chiefly negative—that is, they represent a lack of development in Eusicyoninae beyond the postmysis larval stages identical in both subfamilies.

Many of the supposedly unique features attributed to the Eusicyoninae are either nonexistent or not distinctive. Thus, the group has been stated to have arthrobranchs in a single series, and to lack podobranchs completely, in contrast to all other Penaeidae. The branchial

formula as given by Milne-Edwards and Bouvier, 1909, modified only by recognition of the absence of the epipodite of the third maxillipede from that offered by Bate, 1888, and repeated by Alcock, 1901, Ortmann, 1901, and Borradaile, 1907, is as follows:

Segment	VII	VIII	IX	X	XI	XII	XIII	XIV	Total
Pleurobranch	0	1	1	1	1	1	1	0	} 11 (+rud.).
Arthrobranch	0	1	1	1	1	1	rud.	0	
Podobranch	0	0	0	0	0	0	0	0	} 0 (+5 epipodites)
Epipodite	1	1	0	1	1	1	0	0	

I have examined the branchiae of three specimens of *Eusicyonia dorsalis* (Kingsley), two of *E. stimpsoni* (Bouvier), one of *E. laevigata* (Stimpson), and one of *E. brevirostris* (Stimpson).

As has been correctly noted in the prior formulae, the lamella that occurs at the base of the first maxillipedes of Penaeidae is here unprovided with filaments, and somite XIV bears no branchial appendages at all. I find, however, that there is a total of thirteen functional gills, in addition to the vestigial anterior arthrobranch of somite XIII and the five epipodites, instead of eleven as previously given. The two additional gills occur on VIII and IX. As the two ventral gills of each of these segments are large and conspicuous, it is probable that a minute but plumose gill occurring dorsal and anterior to the other branchiae of each segment is the one that has been omitted from previous descriptions. I find the branchial apparatus of VIII of Eusicyoninae to be completely similar to that of the same somite in all other Penaeidae. The ventral-most gill is attached to the coxa and springs from the anterior side of the base of the epipodite. It is, therefore, clearly a podobranch such as is also present in *Macropetasma* where its presence has been denied by Balss, 1913; and almost certainly in *Atypopeneus*, where it has apparently been described as a second arthrobranch by De Man, 1911. The intermediate gill is clearly an arthrobranch. The minute anterodorsal gill is clearly equivalent to that present in all Penaeidae, but variously termed both arthrobranch and pleurobranch by different investigators. I find that in all Penaeidae this gill is placed dorsal and anterior to the more ventral one, a position uniquely distinctive of pleurobranches, since the upper of a pair of arthrobranches is always placed posterior to the more ventral one. Further, this gill appears later in larval development than the ventral one, and at the same time as the unquestionable pleurobranches of posterior somites where two arthrobranches are already present. Therefore it seems necessary to conclude that the dorsalmost gill of VIII in all Penaeidae, includ-

ing Eusicyoninae, is a pleurobranch, and that the arthrobranch of this somite (as occasionally that of XIII) is unpaired. Although Bouvier, 1908, has stated that a podobranch, a pleurobranch, and two arthrobranches are present on VIII in adult *Funchalia*, Calman, 1925, is not able to find the additional arthrobranch, nor am I. De Man describes two arthrobranches, a pleurobranch, and no podobranch as present on this somite in *Atypopeneus*, but one of his arthrobranches should probably be referred to the last category. Schmitt, 1926a, thinks the dorsal gill of VIII in *Penaeopsis serratus* to be an arthrobranch, and suggests that this and three related species may be separable from the remainder of *Penaeopsis* (*Metapeneus*) by the reported different homology of the dorsal gill. This "difference" is, however, only a matter of term, and is without an actual basis. The branchial formula of VIII is identical in all Penaeidae.

The more dorsal of the two large, conspicuous gills of the body wall of IX cannot be, as given in previous accounts, a pleurobranch, since it is posterior, not anterior, to the more ventral arthrobranch. It is, by its position, the posterior arthrobranch, a supposition completely established by the discovery of the small anterodorsal gill, clearly a pleurobranch set above two arthrobranches as in all other Penaeidae.

The dorsal of the two gills of somite X is attached posteriad the ventral one. As pleurobranches are always placed on the anterior margin of the somite, this gill must be considered as the posterior and dorsal of a pair of arthrobranches, such as are present on this somite in all Penaeidae. The branchial arrangements of somites XI, XII, and XIII are repetitions of X, save that on XIII the anterior arthrobranch is vestigial and un-plumose, just as in many Penaeinae.

Arthrobranches are therefore present in pairs behind VIII, while it is the pleurobranches that are absent from all somites behind IX. This is a more extensive absence than in other Penaeidae, but not startling when it is remembered that these branchiae, present on XIV in Aristaeinae, Solenocerinae, and the *Penaeus* series of Penaeinae, are in *Parapenaeus* and two of the genera of "*Penaeopsis*," and in *Artemesia* of Penaeinae absent from XIV; in *Trachypeneus*, *Xiphopeneus*, *Parapenaeopsis*, *Atypopenaeus*, and one genus of "*Penaeopsis*," and in *Macropetasma* absent from XIII and XIV.

Further, I find that in all Penaeidae the pleurobranches are the last to appear in larval development, contrary to the rule given by Gurney, 1927, who has mistaken the dorsal arthrobranches for pleurobranches. Postmysis larvae of Penaeinae completely lack pleurobranches and are indistinguishable in this from larval Eusicyoninae; in the further course of

development, the Penaeinae add pleurobranches to somites behind VIII and IX, as well as to these somites, while the Eusicyoninae do not develop them behind IX.

The correct branchial formula of *Eusicyonia* is:

Segment	VII	VIII	IX	X	XI	XII	XIII	XIV	Total
Pleurobranch	0	1	1	0	0	0	0	0	} 12 (+rud.)
Arthrobranch	0	1	2	2	2	2	1+rud.	0	
Podobranch	0	1	0	0	0	0	0	0	} 1 (+5)
Epipodite	1	1	0	1	1	1	0	0	

The absence of a fourth, proximal endite from the second maxilla of *Eusicyonia* has been noted by Milne-Edwards and Bouvier, who do not, however, observe the resemblance of this organ to that of *Funchalia*. The absence of exopods from the second and third maxillipeds and walking legs has also been regarded as distinctive of Eusicyoninae. It may be noted that *Macropetasma* and *Artemesia* of Penaeinae lack exopods completely save, respectively, on X and on IX. In all Penaeidae the mysis has a proximal endite on the second maxilla and exopods on all the pereopods. These appendages are lost after the mysis stages in Penaeinae and Eusicyoninae (the postmysis stages of Aristaeinae and Solenocerinae being unknown), and are recovered wholly or in part only late in preadult development in Penaeinae. In Eusicyoninae they do not reappear at all.

The absence of endopods from the pleopods in adult Eusicyoninae is unique in the family. In the mysis of Penaeidae the pleopoda anterior to the uropods are uniramous. An endopod is almost immediately added in Aristaeinae and Solenocerinae, but in Penaeinae the endopod does not appear until late in postmysis development (and it may never develop on the first pleopod of the female where it is of minute size in all Penaeidae where it is present). In Eusicyoninae, endopods never appear except in modified form on the first and second pleopods of the male.

The Eusicyoninae are regarded as displaying a strong resemblance to Aristaeinae in lacking a prosartema from the antennular peduncle and a scale from the lateral section of the ocular somite. In the larval stages of all Penaeidae these projections are lacking. In late larval stages of Penaeinae and presumably of Solenocerinae the ocular scale and antennular prosartema are produced by hypertrophy of the areas that bear them; while in the same way, areas of the median portion of the ocular somite, marked by a pair of low tubercles in some adult Penaeinae

and Aristaeinae, hypertrophy to form elongated stylets in Eusicyoninae.

In late mysis stages of all Penaeidae there are no more than a few setae on the internodistal margin of the carpus of the first chelipeds. To these are later added dense setae, the "special setiferous organ," on carpus and propodus. Milne-Edwards and Bouvier state that these setae are absent in Eusicyoninae. This is true of females, where the special setiferous organ never appears, but males acquire these setae in a form as typical as in either sex of other Penaeidae.

In mysis and early postmysis stages of Penaeinae and Eusicyoninae an anterior-pointing spine is present on sternite XIII, which seems to be absent in the mysis of Aristaeinae and Solenocerinae. In later development a spine is sometimes added to XIV and XII in Penaeinae, while it is added to XII, but apparently not to XIV in Eusicyoninae. Spines on all three somites seem to appear later in aristaeine and solenocerine development. In Penaeinae the spines usually disappear late in development, although the base of that of XIII is retained as part of the median plate of the thelycum. In Eusicyoninae the spines are retained throughout life. The thelycum and petasma of Eusicyoninae, as has been mentioned, are not unique. The sternal position of the male genital openings, supposedly distinctive of Eusicyoninae, is completely reproduced in *Macropetasma* while some degree of migration into the subcoxal membranes occurs in large adults of many Penaeidae. The presence of a dorsal carina on the first pleonic somite of Eusicyoninae is not unique, as it has been described as being, since such carination occurs in *Parapeneopsis sculptilis* (Heller) and several species of *Trachypeneus*. A posterior migration of the rostral teeth on to the carapace occurs more regularly in Eusicyoninae than elsewhere, but is as well marked in some Solenocerinae. The presence of ventral rostral teeth is duplicated in some Solenocerinae and Penaeinae. The reduction of the lateral telson armature of adults (except *Eusicyonia longicauda* Rathbun, in which Stebbing, 1914, states three pairs of mobile spines to be present) to no more than a single pair of fixed teeth is a character found also in Solenocerinae. Postmysis stages of *Eusicyonia* have four pairs of mobile lateral spines, the distal of which become fixed, while one of the mobile pairs may persist even after sexual maturity in some species.

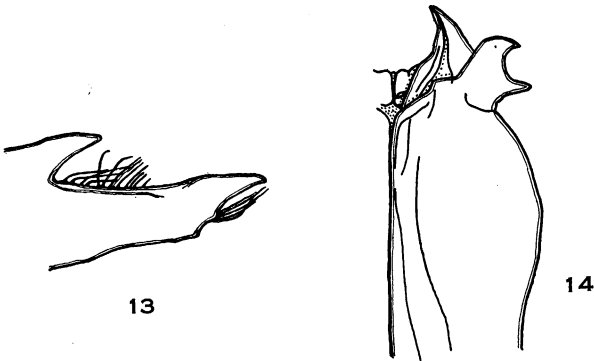


**EUSICYONIA** Stebbing***Eusicyonia dorsalis* (Kingsley)**

Figures 13 and 14

*Sicyonia dorsalis* KINGSLEY, 1878.? *Sicyonia dorsalis* SMITH, 1887; RATHBUN, 1901, part (?); CARY AND SPAULDING, 1909.Not *Sicyonia dorsalis* RATHBUN, 1901, part (?); MILNE-EDWARDS AND BOUVIER, 1909; HAY AND SHORE, 1918.

DISTRIBUTION.—*Eusicyonia dorsalis* has been confused in previous records with a neglected species, *E. stimpsoni*, named from the manuscript of A. Milne-Edwards, but not described, by Bouvier, 1905, and later (Milne-Edwards and Bouvier, 1909) placed in the synonymy of *E.*

Figs. 13-14. *Eusicyonia dorsalis* (Kingsley).

13, rostral tip of female; 14, petasma, left half, distal portion, ventral (posterior) surface.

*dorsalis*. The only definite previous record of *E. dorsalis* is that of the type, by Kingsley, 1878, from the Tortugas, Florida. *E. stimpsoni* seems to be the more abundant species in the West Indies, to judge by the fact that Milne-Edwards and Bouvier's material seems to be referable to it in toto. The numerous records of *E. dorsalis* by Rathbun, 1901, in all likelihood include many referable to *E. stimpsoni*. Specimens of "*E. dorsalis*" from Key West in the collection of the U. S. National Museum, the examination of which was kindly permitted me, appertain to *E. stimpsoni*. The figure of a Beaufort specimen of "*E. dorsalis*" presented by Hay and Shore, 1918, although obscure, seems to represent *E. stimpsoni*. "*Eusicyonia dorsalis*" of Boone, 1930, is certainly not that species, and appears to be *E. laevigata* (Stimpson). The figure of "*E. edwardsi*" from the Caribbean coast of Panama, offered by the same

writer, probably refers to *E. dorsalis*. Whether or not the record of *E. dorsalis* from the western coast of Louisiana, by Cary and Spaulding, based on a determination by the U. S. National Museum, actually refers to that species, I am unable to say, since the material was not available to me; but I am inclined to believe that it does. Other records are indeterminate. I think it probable that *Eusicyonia dorsalis* will be found to have a range roughly parallel to that of *Trachypeneus similis*; and *E. stimpsoni* to *T. constrictus*; a distribution comparable to that of several other pairs of closely related Gulf of Mexico and Caribbean species, and perhaps based on the separation of the former from the latter sea in past geologic time.

STRUCTURE AND NATURAL HISTORY.—A female of 62 mm. in total, 16.5 mm. in carapace length, and a male 57 mm. in total, 14.5 in carapace length, were taken by trawl in the inner littoral about five miles off Pass à la Loutre in late winter and early spring. An immature female 22 mm. in total length was taken from the stomach of a *Raja* off Bayou Scofield in late winter. Mysis and postmysis larvae were taken at the surface in the outer littoral in late spring.

The spine and spine buttress of sternite XIII, present in both male and female, which form the anterior part of the median plate, do not enter into the functional structure of the sperm receptacle. The less elevated posteriorly emarginate hinder portion of the median plate of XIII, as in *Penaeinae* and especially in the *Parapenaeus* series, forms an anterior wall to the transverse depression of XIV from which the sperm receptacles are formed. This sinuous transverse groove of XIV is laterally deeply invaginated as a pair of large membranous sperm sacs, the opening to which is hooded by the produced lips of the posterior margin of the groove, which overlap the posterolateral margins of the median plate. The thelycum differs from that of *Parapenaeus* in that the groove continues anterolaterad the openings of the invaginated sacs and is here not hooded by produced lips. The produced lips are a continuation of an elevated portion of sternite XIV, the anterior slope of which does not reach to the anterolateral continuation of the groove.

The intermediate portion of the vas deferens of the male is a thin-walled simple tube. The contained sperm are not organized into spermatophores, nor embedded in a gelatinous matrix, although refracting granules are scattered through the mass. The spermatozoa resemble those of *Penaeus*, but are of very large size. The male genital aperture is here shifted to the membrane between the coxa and the narrowed sternite of XIV, as in certain other *Penaeidae*. It may be noted that in

the figures of the development of the male genital area of *E. carinata* (Oliv) by Antonnucci, 1930, the structures described by that author as the genital apertures seem to be blind sternal invaginations serving for muscle attachments, placed well anterior to the genital apertures and not in any way connected with them. Antonnucci's "genital papillae" occupy the positions of the apertures of the vas deferens of all specimens of *Eusicyonia* that I have examined.

The petasma appears to be equivalent in some respects to that organ in *Parapenaeus longirostris*, differing by the absence of the inner distal membranous flaps, and by the unproduced anteromedian lobes and the shallowly channeled laterodistal spines. In this latter respect the petasma of *Eusicyonia* resembles that of *Artemesia* and of the *Trachypeneus* series.

VARIATION WITHIN THE SPECIES AND RELATIONSHIP TO OTHERS.—I have had access to the type male of *E. dorsalis* (Kingsley), and the cotype and paratype material, six males and five females, of *E. stimpsoni* (Bouvier) from the Blake dredgings in the West Indies, the careful examination of which was kindly permitted by the Museum of Comparative Zoölogy. I have also examined a male and three females of *E. stimpsoni* from Key West, Florida, in the collection of the U. S. National Museum. The Louisiana specimens are identical with Kingsley's type, and distinct from the other specimens which have been termed "*E. dorsalis*" and for which A. Milne-Edward's manuscript title *E. stimpsoni* must therefore be revived. Milne-Edwards and Bouvier's statement that *E. dorsalis* and *E. stimpsoni* are extremes of an intergrading series seems to be accounted for by the absence of *E. dorsalis* from their material. In the characters discussed by Bouvier—position of the posterior dorsal tooth of the carapace, armature of the rostral tip, length of the rostrum, length of the stylocerite—there is some range of variation within each species. Bouvier appears to have assumed that the extreme of variation in *E. stimpsoni*, which in the above characters approached Kingsley's description, was *E. dorsalis*, and naturally was unable to discover specific distinctions between this and the other extreme of variation in the single species with which he dealt.

The characters of *E. dorsalis* and *E. stimpsoni* are as follows:

The postrostral carina in both species bears two teeth: an anterior placed before the level of the hepatic spine, and a posterior placed anywhere from the midpoint between the anterior tooth and the posterior border to the posterior fourth of the carapace. The posterior tooth is near the midpoint in the available four specimens of *E. dorsalis*, behind it in *E. stimpsoni*. In addition to these two teeth there is the rudiment

of a third dorsal tooth in all the Blake material of *E. stimpsoni*. This rudiment, not mentioned by Bouvier, appears as a minute crestlike swelling a little in front of the posterior tooth, usually with a sharply truncated anterior edge. No trace of this third tooth is found in *E. dorsalis*.

The rostrum of both species bears three dorsal teeth behind the variably armed tip. The posteriormost of these, although not constant in position, is placed well in front of the orbital margin, and is separated by a distinct interval from the anterior tooth of the postrostral series. The tip of the rostrum of *E. stimpsoni* usually appears bifurcate. There is a sixth rostral tooth on the ventral margin, behind the level to which the cleft in the tip extends. The rostral tip of *E. dorsalis*, although it may be termed "simple," differs from that of *E. stimpsoni* only in the emphasis of its parts. Thus, the dorsal prong of the bifid tip has here become greatly enlarged, whereas the ventral element may be rudimentary and the ventral tooth reduced to a blunt angle.

The length of the rostrum is variable in both species, but its point reaches beyond the eye, and sometimes considerably beyond. In all available specimens of *E. dorsalis*, the rostrum extends horizontally or below the horizontal, while in all of *E. stimpsoni*, it is elevated at a considerable angle. The ridge on the lateral surface of the rostrum of *E. dorsalis* slopes upward to near the dorsal margin, while in *E. stimpsoni* the ridge runs near to and parallel with the ventral margin.

The antennal angle in both species is armed with a spine which seems to be longer in *E. dorsalis*, and with a more conspicuous post-marginal buttress.

The carapace of *E. dorsalis* in specimens of all sizes is less deep and inflated than that of *E. stimpsoni*.

The margins of the clefts at the posterior ends of the carinae of the pleonic terga of *E. dorsalis* may be produced on somites 3, 4, and 5 into long slender spines, whereas in *E. stimpsoni* they never seem to be more than short angular projections.

The anteroventral margins of the pleura of the first pleonic somite of *E. dorsalis* are always concave or at least (as in the smallest Louisiana specimen) are straight, with an anterior angle in addition to one in the middle of the ventral edge. In *E. stimpsoni* the anteroventral margins of the pleura are somewhat convex, and there is no angle anterior to that at the middle of the ventral edge of the pleuron. The posterior angles of somite 1 may be produced into dentiform projections in both species. The pleura of somites 2, 3, and 4 in *E. dorsalis* have a straight, truncate

ventral margin with both an anterior and a posterior angle, the former of which may be sharp, while the latter may be armed with strong curved spines. In *E. stimpsoni* the ventral margins of these pleura curve upward without a definite posterior angle, and the posteriorly directed spines characteristic of *E. dorsalis* seem never to occur on the equivalent marginal area of *E. stimpsoni*. The pleural angles become better defined, and pleural spines appear and increase in size from behind forward in direct ratio to increase in size. Only slight differences can be found in the pleural margins of individuals of the two species under 25 mm., at which size some of the pleura are unarmed at points that bear spines in the adult.

The thelycum is different in the two species, although variable individually and subject to considerable growth changes in both. The subrectangular elevated areas placed one on each side of the median line of the fourteenth sternite of *E. dorsalis* are longer than broad, and with the depression included between them form almost a square. Their lateral margins project little beyond the margin of the median plate. In *E. stimpsoni* the plates are broader than long, and together form a rectangle much shorter and broader than in *E. dorsalis*. The lateral margins of these elevations often project much beyond the lateral margins of the median plate. Bouvier's figure of this organ in *E. stimpsoni* is found to be inaccurate, on comparison with the specimen from which it was derived.

The mandibular palps of *E. dorsalis* taper considerably to a narrow tip that is truncated obliquely enough so that the sharp lateral margin extends distinctly distad the median margin. In *E. stimpsoni* the tip of the palp is much broader, its truncation is more transverse, and the lateroterminal angle is rounded. The outline of the depression of the external surface of the basal segment of the palp differs in the two species, the proximal median margin being convex outward in *E. dorsalis* and convex inward in *E. stimpsoni*.

In the petasma of the Louisiana male and in that of Stimpson's type, a smaller specimen about 40 mm. in total length, the projecting tooth of the posterior surface of the distal end of the petasma is bifurcate, its distal prong curving proximad, while its proximal prong, which is as large and conspicuous as the distal one, curves distad. The petasma of all seven available males of *E. stimpsoni*, the largest of which was about 34 mm. in total length, bore an unfurcate tooth.

The distinctions between *E. dorsalis* and *E. stimpsoni* seem to be completely reproduced in Pacific America by an undescribed species

and *E. picta* Faxon. These four species, together with the Pacific American *E. affinis* Faxon and the Indo-Pacific *E. benthophila* De Man (which is perhaps related to *E. affinis* rather than, as De Man has it, to *E. picta*), are, so far as I can determine, the only species of the genus with only two postrostral teeth behind the orbital margin, of which one lies anterior to the level of the hepatic spine.

### SERGESTIDAE Dana

#### Sergestinae Bate

#### ACETES H. Milne-Edwards

*Acetes carolinae* Hansen and *A. americanus* Ortmann (*A. brasiliensis* Hansen) may be regarded as forming a subdivision of *Acetes*, distinguished from the remaining species of the genus by the lack of a second rostral tooth between the rostral tip and the posterior tooth, the absence of a stout distally directed spine or spines from the proximal part of the inferior antennular flagellum of the male, and the absence of a podobranch from the second maxillipeds. Hansen has stated that a podobranch is present on this somite throughout the genus. Kemp, 1917, finds this description applicable to the Indo-Pacific species, but Ortmann, 1893, states that a podobranch is absent from the second maxillipeds of *A. americanus*. I do not find a podobranch in *A. carolinae*.

The second division seems to contain eight species, of which one, *A. paraguayensis* Hansen, occurs in the American South Atlantic.

The remaining species of the second division occur in the Indo-Pacific, and may be listed as follows:

1.—*A. serrulatus* (Kröyer), Hansen, 1919, with which *A. insularis* Kemp, 1917, seems synonymous.

2.—*A. indicus* H. Milne-Edwards, Kemp, 1917, with which *A. spiniger* Hansen seems synonymous.

3.—*A. sibogae* Hansen, which perhaps includes the specimens reported by Kemp as dimorphic males of *A. erythraeus* Nobili with elongate third segment of the antennular peduncle.

4.—*A. erythraeus* Nobili, Kemp, 1917, with which *Acetes* species Hansen seems synonymous. I have examined a male of this species from French Somaliland.

5.—*A. vulgaris* Hansen, which seems to differ somewhat from *A. erythraeus* by its more numerous series of spines of different arrangement on the fifth joint of the lower antennular flagellum of the male, and the absence of a lobule from the segment in front of the clasping spine; the presence of a spine at the distal inner angle of the coxa of the third legs in the male, and the absence, as figured, of a spine from the outer margin of the exopod of the uropod; and the longer median lobe of the capitulum of the petasma, which bears three large spines and lacks the numerous smaller ones of *A. erythraeus*, except near the tip. Hansen reports that the female bears a pair of sternal

protuberances between the coxae of the third legs, which are absent in *A. erythraeus*, but faint elevations in this position are figured by Kemp for the latter species.

6.—*A. chinensis* Hansen, apparently related to *A. japonicus*, but of which the characters are as yet incompletely known.

7.—*A. japonicus* Kishinouye, Kemp, 1917, with which *A. dispar* Hansen seems to be synonymous. A negative distinction is made by Hansen between his form and Kishinouye's: that the sexual difference in the third segment of the antennular peduncle of *A. dispar* could not have been overlooked by Kishinouye if present in *A. japonicus*. This means of differentiation seems to be doubtful in view of Kemp's examination of Japanese material, which he finds identical with Indian specimens, and which therefore displays sexual differences in the peduncle. Kemp further notes variation in the length of the processus ventralis of the petasma sufficient to obscure the differences mentioned by Hansen.

I have examined a female of *A. japonicus* from Port Swettenham, Selangor, which differs from Kemp's description and figures as follows: The sides of the posterior free projection of the genital plate are parallel rather than convergent; the posterolateral corners are rounded rather than angular; the emargination of the posterior margin of the projection is of about the same depth as in Kemp's figure, but the breadth of the projection along its posterior margin is only about one-third greater than its length in the midline, rather than nearly one-half. The projection is elevated along its midline rather than depressed; it is also slightly elevated along the posterior margin. The projection of the plate does not extend back to the transverse furrow. Mediad the coxae of the third legs on each side is a low pyramidal projection of the sternum. The projection of the proximal inner corner of the coxa of the third legs is two-headed, as figured by Kemp, but the posterolateral head is placed much farther laterad the anteromedian one. The laterodistal margins of the tip of the telson bear a minute tooth on one side, the mate to which is absent from the other. I think it probable that, as in *A. carolinae*, the telson armature, petasma, and female genital plate of *A. japonicus* are somewhat variable with age, individual, and locality. The characters exhibited by the specimen described above appear to bridge the slight differences between *A. dispar* Hansen and *A. dispar* var. *vel* sp. n. Hansen; and between these and *A. japonicus* as described by Kemp.

It may be noted that the "somewhat or much restricted" geographical distribution of the species of *Acetes* postulated by Hansen does not appear to be more so than in other littoral, as compared with other oceanic, penaeids.

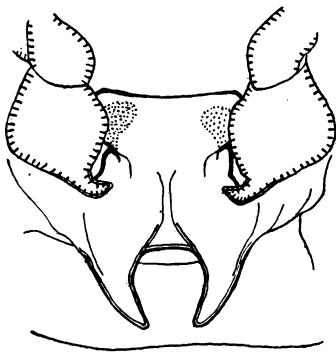
## Division 1

**Acetes carolinae** Hansen

## Figure 15

*Acetes carolinae* HANSEN, 1933.*Acetes* sp. BROOKS, 1882.

DISTRIBUTION.—The present material, of which a description was in press when Dr. Hansen's careful study appeared, is certainly identical with that which he describes from the North Carolina coast, although some slight differences may indicate that it is a local race. The fact that larval and postlarval stages of an unnamed *Acetes*, undoubtedly identical with the present one, have been reported from the type locality by Brooks, 1882, is not mentioned by Hansen.



15

Fig. 15. *Acetes carolinae* Hansen.  
Sternum of 12th and 13th somites of female.

NATURAL HISTORY.—An abundant material ranging in total length from 6 to 17 mm., was obtained along the Louisiana coast from the Mississippi River west to Timbalier Island. The area of greatest abundance of adults was the shallow, variably brackish coastal zone of the inner littoral, but some individuals occurred in the inside waters close to the coast. A few adults and the larval stages from the protozoëa were taken at the surface in the outer littoral in spring.

STRUCTURE.—The oviducts of the female open by a transverse slit just above the coxal projection of each third leg, on the posteromedian surface of the joint. Along the proximal inner margin of the coxa a fleshy lamella running forward from just anterior to the coxal projection overlaps the lateral margin of the sternite. Mediad the lamella,



and overhung by it, a deep narrow longitudinal groove runs nearly to the anterior edge of the sternite. In the anterior end of this channel on either side lies the opening of an invaginated sac, the sperm receptacle. In impregnated females each sac contains a mass of sperm enclosed in a matrix of clear yellow-brown secretion, and may be seen to run postero-medial beneath the sternum from its aperture. The sacs are elliptical in outline and extend back less than half the distance from the anterior margin of the sternite to the posterior margin of the third leg. The groove is evidently the channel, almost closed in by the coxal lamella, by which sperm pass to the oviduct opening. The posterior half of the median margin of the groove is elevated into a liplike ridge. The curved coxal projection abuts against the posterior part of this lip, and forms with it a retaining wall behind and rising as high as the opening of the oviduct. Behind the posterior part of the lip is a narrow crescentic transverse depression of the sternum.

This apparatus is very like that of *Sergestes*, the description of which by Hansen, 1922, is in error. The "opercule" of *Sergestes* is a transverse fold of the genital sternum, not "entre le segment génital et le précédent," which arches back over the openings of the sperm receptacles that lie near its lateral ends. This fold is absent in *Acetes*. The openings of the oviducts are situated, as in *Acetes*, above the projecting proximo-medial corner of the coxa, instead of "en dedans des coxae . . . entre ceux-ci et le sternum." The "duplicature du tégument" is identical with the coxal lamella described in *Acetes* and does not cover the oviduct aperture. The channel between it and the sternite leads forward to the lateral edges of the operculum. The channels lack any decided median lips, but on their posterior median margins on each side stand two toothlike projections, from between which a depression runs antero-medial to the middle of the operculum. This description is prepared from *Sergestes arcticus* Kröyer.

The distal portions of the vasa deferentia of the male of *Acetes* are much enlarged. The swollen terminal parts protrude as prominences of the sternum which have been termed "genital coxae," although they appear to correspond only to the evaginated subcoxal membranes that cover the protruding distal parts of the vasa deferentia of *Sergestes*. The spermatophores lie in the anterolateral parts of the prominences, at the tips of which there is a very narrow obliquely transverse slitlike opening. The two genital prominences are separated by a narrow median depression. Posterior to the spermatophore within the vas is a large plate of clear brown spermfree material; the wall of the vas is here

thickened, and seems to secrete the plate. In the part of the vas dorsal to the secretion mass an incomplete spermatophore usually occurs.

The completed spermatophore, like that of *Lucifer*, is gourd-shaped, with a slender curved upper portion. It consists of a thin outer wall sheathing a mass of sperm in a matrix of clear yellow sperm-free material. The minute sperm are cigar-shaped, with a refracting spherule at one end. The sperm mass found in the female receptacle appears to represent the contents of the spermatophore without the sheath. The neck of the sheath is probably inserted into the receptacle, and the contents of the enlarged part discharged through it, as has been reported for *Lucifer*.

The sperm receptacles of the Sergestidae, paired invaginations of sternite XII, are not homologous to those that occur in some Penaeidae. The spermatophores of the latter family may be attached along sternites XIV, XIII and the posterior part of XII in species without an enclosed receptacle, but invaginated receptacles are usually formed from the posterior part of sternite XIII and from sternite XIV.

VARIAION WITHIN THE SPECIES AND RELATION TO OTHERS.—*Acetes carolinae* is very closely related to *A. americanus* Ortmann, 1893, from northern Brazil, with which *A. brasiliensis* Hansen, 1919, is probably synonymous. The characters by which Hansen has distinguished *A. brasiliensis* from *A. americanus* seem of very uncertain importance. The differences in length of the ciliated part of the external margin of the exopod of the uropod, as those in other characters not mentioned by Hansen, are perhaps attributable to the obvious inaccuracy of Ortmann's figure. That Ortmann failed to notice the elongation of the third segment of the antennular peduncle of the male of his species is no more astonishing than that Kishinouye failed to do so for *A. japonicus*, as Kemp has shown to be the fact. It is true that one of the species of *Acetes* differs most conspicuously from a related form by a lack of elongation of the antennular peduncle of the male. However, I do not believe that the failure of an earlier worker to mention a sexual dimorphism, not in his time emphasized as of taxonomic significance, can be regarded as sufficient to establish the specific distinctness of a form displaying this dimorphism, until the actual existence of a related species without such sexual difference is demonstrated.

The following notes may be added to Hansen's description of *A. carolinae*:

The base of the lower flagellum of the antennule of the male does not constantly display the characters described by Hansen for Atlantic specimens. The large, distal, proximally curved spine is often longer,

slenderer, less curved, and with a less swollen base than in Hansen's figure; and may be separated from the others by an interval as great as that figured by Hansen for *A. americanus*. The number of proximal spines is sometimes reduced to five. The spines of this series become less curved and have less obtuse and scabrous tips from proximal to distal, but the sharp distinction between a proximal four spines and a distal two described by Hansen is not constantly maintained. The two spines laterad the second of this series, described and figured by Hansen for *A. americanus* but not for *A. carolinae*, are present. There is a short stout dorsal spine on the sixth segment of the inferior antennular flagellum.

The superior antennular flagellum of the male is over half as long as the individual, and twice as long as that of the female.

The capitulum of pars media of the petasma of Louisiana material is much less clearly distinct from that figured by Hansen for *A. americanus* than is the case with figures and description of the North Carolina material. The inner lobe, although shorter than in the figures of the Brazilian species, presents much the same appearance, and is conspicuously longer than in the figured Carolina specimen. It is broad but flat, and its flat surface is curved laterad, arching over the next lobe. This lobe appears occasionally to be armed with more than two spines. The spines are not acute, as figured by Hansen for both *A. americanus* and *A. carolinae*, but are spatulate, with a truncated tip, like the spine of the proximal of the three lateral lobes of the capitulum. The tip of the most distal of these lateral lobes is produced into a flattened spinelike projection with a serrated, truncate distal margin, as is the most proximal, the projection of which appears bifurcate only because of the refractiveness of its thickened margins. The capitulum thus differs from that of the Brazilian form only by its shorter distal lobe with variable but sparser armature, and the variably flattened nature of the projecting tips of the distal and proximal lateral lobes. The midsection of pars media is less expanded than in the Brazilian form; but its lateral margin is convex, not concave as in the figure of *A. carolinae*. The pars externa, although variable in length, reaches above the base of the capitulum only in some smaller individuals; it is, however, longer than in the figure of *A. carolinae*.

The genital plate of all Louisiana females differs from that figured by Hansen in that the posterolateral projections appear as prolongations of the lateral angles of a truncated posterior margin, the margin between the projections being usually as wide as or wider than the length of the projections, and much less concave than in Hansen's figure of *A. carolinae*. In only a few specimens are the projections as long and as close together

as in the one here figured, which still appears quite different from the Carolina representative. This difference is probably an expression of geographical variation. The posterolateral projections are conspicuous even in quite small females of 9 mm. total length. The proximal inner corner of the coxa of the third legs projects, not as "an obtuse protuberance" but as a flat semirectangular plate with a sharp distomedian corner.

The tip of the telson, which in Ortmann's figure of *A. americanus* bears eight stout setae and no spines, is variable in *A. carolinae*. In some specimens a pair of small spines are borne at the laterodistal angles, which they then define. The terminal margin may be either convex or slightly concave, and the setae vary in number from three to ten.

It may be noted that the antennal flagella differ from those of *A. japonicus* as described by Kishinouye, 1905, in that the paired setae of the segments distad the flexure are plumed and arched over toward one another, thus forming the walls of a hollow cylinder of larger diameter than the flagellum. Between the bases of the setae of each pair is a short straight seta projecting into the cylinder.

The coloration of *A. carolinae* is quite similar to that described for *A. japonicus*, but bright red spots occur at the bases of other appendages as well as the uropods.

Although I do not consider the differences here pointed out sufficiently certain or significant to necessitate taxonomic recognition, should direct comparisons prove this to be desirable, I would suggest for Louisiana material the subspecific name *Acetes carolinae louisianensis*.

### **Luciferinae Bate**

#### **LUCIFER** Thompson

#### **Lucifer faxoni** Borradaile

*Lucifer faxoni* BORRADAILE, 1915; HANSEN, 1919 and 1922.

This cosmopolitan species, which Hansen regards as not strictly oceanic, has not been previously recorded from Louisiana. The species was taken in great abundance in the outer littoral where, in addition to mature males and females, larval stages from the protozoëa on were obtained. The males seemed to be more numerous proportionately to the females than is usual among Penaeidea. The species was also found throughout the inner littoral, and in the estuarine waters near the sea. It occurred from surface to bottom, to the greatest depth of the area investigated, 25 fathoms.

One female bearing six large ova attached by long thin bands to the third legs above the ischium was taken in the outer littoral.

The dissection of a number of specimens indicates that the descriptions of the internal genital apparatus by Brooks, 1882, and Bate, 1888, are incorrect, and that the definition of the subfamily by Hansen, 1922, as with "Un seule ouverture génitale impaire dans chaque sexe" is without foundation.

The minuteness of the animals and the delicacy of the integument are such that the genital apertures are not readily discovered in either sex. Those of the female appear to open on the posteromedian surface of the coxa in a position equivalent to that in *Acetes*. The ovary is paired, the laterally flattened ova of each tube being in single file, and appressed against the ova of the opposite tube. After entering the pereion, the tubes turn downward, diverge, and enter the musculature of the body wall on each side just anterior to the third legs. The paired, pear-shaped, saclike sperm receptacles lie side by side in the protruding posterior portion of the pereionic sternum, which they fill in impregnated females. The sacs open separately between the third legs into a common atrium formed by a median depression of the sternum.

In all the males that I have examined, the vas deferens of either one side or the other is in use, but not that of both. The empty vas of the other side shows no signs of atrophy. The terminal portion of the vas is occupied by a spermatophore like that described for *Acetes*, except that the blunt distal end of the sheath usually contains a clear brown sperm-free mass, while the tapering upper part is filled with a mass of sperm that is not surrounded by a sperm-free matrix. Occasionally the sperm mass seems to fill the sheath completely. The upper, pleonic portion of the vas usually contains a cylinder of sperm bound together by a clear secretion; and a mass of clear brown sperm-free material, the two representing the contents of the spermatophore sheath, which is evidently secreted by the terminal part of the vas. The genital prominences, separated by a deep median depression, appear to open at their anteromedian ends, but I was unable clearly to make out the apertures, which are difficult to see even in the large males of *Sergestes*. Within each receptacle of the female is found a disc of clear material surrounded by extremely minute sperm, which mass seems to be equivalent to the contents only of a spermatophore sheath. I have not observed a female to which a sheath is attached. I think it probable that a separate spermatophore is necessary for filling each of the pair of receptacles. Since each male carries but one complete spermatophore at a time, apparently an adaptation to

the great lateral compression of its body, it is probable that two matings occur, with different males, which perhaps accounts for the unusually great abundance of that sex.

The specimens examined differ very little from the descriptions and figures of *Lucifer faxoni* given by Hansen, and appear clearly distinct from the related Pacific form, *L. hanseni* Nobili, as described.

## SUMMARY AND CONCLUSIONS

### TAXONOMY

#### PENAEIDAE.

The subfamily Solenocerinae Wood-Mason and Alcock is re-established. The subfamily Penaeinae is redefined. The name Sicyoninae Ortmann is altered to Eusicyoninae. The relations between the four subfamilies and the characters of each are discussed, particularly in the light of larval history. Aristaeinae and Solenocerinae display strong affinities and are contrasted to a second closely bound group composed of Penaeinae and Eusicyoninae.

I. Solenocerinae.—The genus *Solenocera* Lucas is reviewed. *Parasolenocera* Alcock cannot be maintained as a distinct genus. *Solenocera* (*Parasolenocera*) *maldivensis* Borradaile is a peculiar form for which the new subgenus *Transolenocera* is proposed. The possibility is pointed out that *Solenocera africanus* Stebbing includes more than one species. *Solenocera vioscai*, new species, is described from Louisiana, and specimens from Venezuela heretofore regarded as *S. membranacea* H. Milne-Edwards are referred to it.

II. Penaeinae.—The subfamily is composed of four series of genera centered about *Penaeus* Fabricius, *Trachypeneus* Alcock, *Parapenaeus* Smith, and *Macropetasma* Stebbing.

1. *Penaeus* Series.—The new subgenus *Pelagopenaeus* of *Funchalia* Johnson is proposed for the reception of two species hitherto placed in *Penaeus*. *Penaeus* is composed of two superspecific groups of which the American *P. setiferus* (Linnaeus) and *P. brasiliensis* Latreille are respectively the primitive members. Geographical and individual variation within these two species and their relations to nearly allied Pacific-American species are discussed. *P. vannamei* Boone is redescribed and is distinguished from *P. occidentalis* Streets and *P. stylirostris* Stimpson.

2. *Trachypeneus* Series.—The characters of the six genera included are described. Two have not hitherto been distinguished from one another or from the third, parapeneine, genus with which they have been confused under the name *Penaeopsis* Bate. *Trachypeneus* is composed of two superspecific groups, the first of which is further subdivided. *T. similis* (Smith) and *T. constrictus* (Stimpson) are distinct species. The definition of *Xiphopeneus* is amended in

recognition of the fact that the adult lacks the transverse carapacic suture characteristic of other forms with a longitudinal suture. Geographical and individual variation within *X. kroyeri* (Heller) is discussed. The Pacific American *X. riveti* Bouvier is no more than varietally distinct from the Atlantic species.

3. *Parapenaeus* Series.—The three genera included are discussed. *Parapenaeus* is redefined and reviewed. *Parapenaeus politus* (Smith) and "*Penaeopsis*" *paradoxus* (Bouvier) are synonymous with *Parapenaeus longirostris* (Lucas).

III. Eusicyoninae.—The manuscript species of A. Milne-Edwards, *Eusicyonia stimpsoni* (Bouvier), is specifically distinct from *E. dorsalis* (Kingsley) with which it has been synonymized. Individual variation within these species and their relations to other members of the genus are discussed.

#### SERGESTIDAE.

I. Sergestinae.—The genus *Acetes* is composed of two super-specific groups, each of which is reviewed. *A. brasiliensis* Hansen appears to be synonymous with *A. americanus* Ortmann; *A. insularis* Kemp with *A. serrulatus* (Kröyer); *A. spiniger* Hansen with *A. indicus* H. Milne-Edwards; *A. dispar* Hansen and *A. dispar* variety *vel* sp. n. Hansen with *A. japonicus* Kishinouye; *A. erythraeus* [Nobili] Kemp, part, with *A. sibogae* Hansen; *A. species* Hansen with *A. erythraeus* Nobili.

II. Luciferinae.—The definition of the subfamily is amended in recognition of the paired nature of the genital apertures.

### MORPHOLOGY

#### PENAEIDAE.

The nature and development of significant structures is described.

##### I. BRANCHIAL APPENDAGES.

The respiratory exite of somite VII is constantly present but may or may not be provided with filaments. Somite VIII constantly bears an epipodite and a podobranch, one arthrobranch, and a pleurobranch. Somites IX–XII constantly bear two arthrobranches in addition to a variable number of other gills. Somite XIII bears one or two arthrobranches of which the anterior when present may be devoid of filaments. Somites behind IX bear pleurobranches in other Penaeidae than the Eusicyoninae. The epipodites of Aristaeinae and Solenocerinae are characterized by weak or obsolete furcation which seems otherwise to occur only in the first, trachypeneine, genus of the conglomerate *Penaeopsis*. The branchiae of Aristaeinae and Solenocerinae appear earlier in development than do those of Penaeinae and Eusicyoninae. The pleurobranches are the last gills to appear.

## II. NONBRANCHIAL APPENDAGES.

1. The proximal endite of the second maxilla and the exopodites of the maxillipeds and pereopods are present in the mysis stages of all Penaeidae. In postmysis stages of Penaeinae and Eusicyoninae (these stages in Aristaeinae and Solenocerinae being unknown) the appendages mentioned are completely lost, while in later stages they are wholly or in part recovered. The almost complete absence of these structures in Eusicyoninae represents nondevelopment beyond postmysis characters. There are minute exopods on the pereopods of *Parapenaeus*.

2. The pleopods in advance of the uropoda are uniramous at their first appearance. Endopods are almost immediately added in the mysis of Aristaeinae and Solenocerinae; are added late in postmysis development in Penaeinae; and are never added in Eusicyoninae except in modified form on the first and second male pleopods.

3. The tubercle of the ocular peduncle, conspicuously projecting in most Aristaeinae and Solenocerinae, is represented by more or less marked external vestiges in Penaeinae, lacking in Eusicyoninae. It attains its development subsequent to the mysis stages.

4. A strong spine occurs on the median margin of the basal segment of the antennular peduncle in the mysis of Penaeidae. This spine disappears in later stages of all except the members of the *Parapenaeus* series. An elongated free scale is produced from the internal margin of the basal segment of the antennular peduncle during the postmysis development of Penaeinae and Solenocerinae, an unhypertrophied, setose homologue of which is present in other Penaeidae.

5. The setiferous organ of the carpus and propodus of the first chelipeds is absent in the larval stages of all Penaeidae but appears during postmysis development in all but the females of Eusicyoninae.

## III. CEPHALOTHORAX.

1. Ocular Somite.—The conspicuous pair of lateral scales of Penaeinae and Solenocerinae and of median stylets in Eusicyoninae are hypertrophied during postmysis development. They are represented by unenlarged homologous projections in many other adult Penaeidae.

2. Carapace.—Postorbital spines occur in adult Solenocerinae alone. Ventral rostral teeth occur in some species of all of the subfamilies but the Aristaeinae and are probably anterior teeth secondarily occupying a ventral position through the hypertrophy of posterior teeth into a false tip. Postrostral teeth behind the level of the cervical suture occur in Eusicyoninae and some Solenocerinae. Both, either, or neither longitudinal and transverse sutures occur on the carapace of Penaeinae. The transverse suture, absent in adults of *Xiphopenaeus*, is present in preadult stages.

3. Pereionic Sternum.—A median spine is variably present on sternites XII, XIII, and XIV in Penaeidae. That of XIII appears to occur in the mysis of Penaeinae and Eusicyoninae, but not of Aristaeinae and Solenocerinae. Spines or traces of them may sometimes be present on all three segments of adults of the latter two subfamilies. In addition to that of XIII, a spine usually appears on XIV in the postmysis stages of Penaeinae, and sometimes on XII;



all three spines are usually later lost, although the buttress of that of XIII takes part in the formation of the median plate of the thelycum. A spine on XIV seems not to occur in Eusicyoninae, in which those of XIII and XII are present in the adult.

A pair of spines or lamellae at the posterior margins of sternites X–XIV may be conspicuous, present, or absent in Penaeidae. From those of XIII are probably derived the functionally important posterior portion of the median plate of the thelycum.

#### IV. PLEON.

1. Telson.—The early telson of Penaeidae is posteriorly forked or deeply emarginated, with a variable number of pairs of spines on the lateral and posterior margins, of which the fourth spine from the base is usually enlarged. This type of telson is present in late mysis stages of Aristaeinae and Solenocerinae. In Penaeinae and Eusicyoninae the earlier type is modified in mysis stages to a form posteriorly truncated between the enlarged fourth lateral spines. In later development a median terminal spine appears which becomes extremely large in the adults of these two subfamilies, and in Solenocerinae. In adult Aristaeinae the telson is truncated or with a weak terminal point. The lateral spines in Penaeidae may be completely lost or may be retained in various numbers. In a few adult Penaeinae there are more than four pairs of spines. The distal pair in adults may be fixed or mobile; they are fixed in Solenocerinae and Eusicyoninae where the preceding pairs are usually absent; and in the *Parapenaeus* series where one or more anterior pairs of mobile spines are present.

#### V. GENITAL APPARATUS.

1. Thelycum.—The sperm receptacle is open in most Aristaeinae, the Solenocerinae, and some species of the *Penaeus* series of Penaeinae; in all of which a large pair of more or less complex spermatophores is attached to the posterior sternites of the female. In other Penaeidae a depressed anterior belt of sternite XIV, the homologue of which is present in many species with open thelycum, is invaginated in various ways to produce unpaired median or paired lateral enclosed sperm receptacles.

2. Spermatophores.—Relatively simple paired spermatophores, in which rudiments of an attachment apparatus such as is present in the externally applied spermatophores are sometimes discernible, occur in many Penaeidae with enclosed receptacle; sperm-free material, possibly homologous to the appendages, may in others seal the female receptacle. In some members of the *Trachypeneus* series of Penaeinae the spermatozoa are packed in numerous minute subspherical sacs. The male genital apertures may be sternal in Penaeinae as well as in Eusicyoninae.

3. Petasma.—The copulatory endopods of the male first pleopods are of three types: The simplest, open form of petasma occurs in Aristaeinae, Solenocerinae, and some Penaeinae; a semitubular petasma with a pair of produced, deeply channeled laterodistal spouts occurs in the *Trachypeneus* series of Penaeinae; a semitubular petasma with two pairs, lateral and posterior, of distal spines and appended lamellae, the lateral of which are not deeply channeled for sperm conduction, occurs in some Penaeinae and the Eusicyoninae.

## SERGESTIDAE.

A podobranch is lacking from the second maxillipeds of *Acetes carolinae* Hansen. The sperm receptacles of Sergestidae, paired invaginations of sternite XII, do not appear to be homologous to those of most Penaeidae, which occur on somite XIV. The oviducts seem universally to open on the coxae of the third legs as in other Penaeidea. The ovary of *Lucifer* is paired.

## NATURAL HISTORY

The region investigated is described. All of the peneids discussed occur in the inner littoral zone, although *Solenocera* and *Parapenaeus* appear usually to inhabit the waters further offshore. All of the peneids taken seem to spend at least a part of their history, usually the breeding period and early larval stages, in the outer littoral zone where larvae of several species not occurring closer to shore were also found. It is suggested that *Penaeus setiferus* and *P. brasiliensis* may spend their adult life in the outer littoral. Immature individuals of the two species of *Penaeus* only are regular inhabitants of the inside waters, although other species occasionally enter the seaward portion of this area.

It is suggested that *Solenocera* is a burrowing form in which respiratory water is supplied through the antennular conduit by a reversal of the usual direction of decapod branchial current.

The bionomics and especially the sexual dynamics of *Penaeus setiferus* and *P. brasiliensis*, as well as of other forms, are described. It is possible that both of the species of *Penaeus* live and are sexually active for more than one season. The range of *Penaeus setiferus*, extended northward by a new record, is less extensive and its distribution within this range more localized than that of *P. brasiliensis*. This distribution is perhaps in part conditional upon a greater relative dependence upon estuarine conditions in the former than in the latter species.

## BIBLIOGRAPHY

- ALCOCK, A. 1901. 'Descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala in the Indian Museum.' Calcutta.
1905. 'Revision of the genus *Peneus*.' Ann. Nat. Hist., (7) XVI.
1906. 'Catalogue of the Indian decapod Crustacea in the collection of the Indian Museum.' Part III, Macrura. Fasc. I. The prawns of the *Peneus* Group. Calcutta.
- ANDREWS, E. A. 1911. 'Sperm transfer in certain decapods.' Proc. U. S. National Museum, XXXIX.
- ANTONUCCI, E. 1930. 'Sullo sviluppo di caratteri sessuali esterni nei due sessi di *Sicyonia sculpta*.' Arch. Zool. Ital. Torino, XIV.
- BALSS, H. 1913. 'Decapode Crustaceen.' In Schulte, 'Zool. anthropol. Ergeb. Forsch. Westlichen und Zentralen Südafrika, Band 5,' Denkschriften med.-naturw. Gesellschaft Jena, XVII.
1914. 'Ostasiatische Decapoden. II. Die Natantia und Reptantia.' Abh. math.-phys. Kl. Akademie der Wissenschaften, II, Suppl. Band, Abh. 10.
1925. 'Macrura 2. Natantia. Teil A.' Wissenschaftl. Ergeb. der Deutsche Tiefsee-Expedition. XX. Jena.
- BATE, C. SPENCE. 1881. 'On the Penaeidea.' Ann. Nat. Hist., (5) VII.
1888. 'Report on the Crustacea Macrura collected by H. M. S. "Challenger" during the years 1873-1876.' Rep. 'Challenger' Exped., Zoology, XXIV. London.
- BENEDICT, J. E. 1894. 'Notice of crustaceans collected by the U. S. scientific expedition to West Africa.' Proc. U. S. National Museum, XVI.
- BOONE, L. 1930. 'Scientific results yachts "Eagle" and "Ara." Crustacea.' Bull. Vanderbilt Marine Museum, III.
1931. 'Anomuran, Macruran Crustacea from Panama and Canal Zone.' Bull. Amer. Mus. Nat. Hist., LXIII, Art. 2.
- BORRADAILE, L. A. 1907. 'On the classification of the decapod crustaceans.' Ann. Nat. Hist., (7) XIX.
1910. 'Penaeidea, Stenopidea and Reptantia from the western Indian Ocean.' Trans. Linn. Soc. London, Series 2, Zool., XIII, part 2.
1915. 'On the species of *Lucifer* and their distribution.' Ann. Mag. Nat. Hist., (8) XVI.
1916. 'Crustacea. Part I. Decapoda.' British Antarctic ('Terra Nova') Exped. 1910, Nat. Hist. Rept., Zoology, III, No. 2.
- BOUVIER, E. L. 1905. 'Macroures Nageures du Blake et du Hassler.' C. R. Acad. Sci., CXLI.
1907. 'Crustacés décapodes nouveaux recueillis a Paita (Perou).' Bull. Mus. d'Hist. Nat., Paris, II.
1908. 'Crustacés décapodes (Pénéides) provenant des campagnes des yachts "Hirondelle" et "Princesse Alice" (1885-1915).' Res. Camp. Sci. Monaco, XXXIII.
- BRITO CAPELLO, F. DE. 1864. 'Descrição de tres especies novas de Crustaceos de Africa occidental e observações acerca do *Penaeus bocagei*.' Lisboa.
- BROOKS, W. K. 1882. 'Lucifer, a study in morphology.' Phil. Trans. Royal Soc. London, CLXXIII, Art. 1.

- CALMAN, W. T. 1925. 'On macrurous decapod Crustacea collected in South African waters.' Special report No. III. Fisheries and Marine Biological Survey, IV. Capetown.
- CARY, L. R., AND SPAULDING, H. M. 1909. 'Further contributions to the marine fauna of the Louisiana coast.' Bull. Gulf Biologic Station, XII. Baton Rouge.
- DE HAAN, W. 1850. 'Crustacea.' In 'Fauna Japonica de Siebold.' Leyden.
- DE MAN, J. G. 1887. 'Bericht über Decapoden und Stomatopoden.' Archiv. f. Naturg., XLIII, Art. 1.
1911. 'Decapoda of the Siboga Expedition. Part I. Family Penaeidae.' Siboga-Expeditie XXXIX a. Leyden.
1925. 'Décapodes Macroures marins et fluviatiles du Bassin du Congo Belge.' Mus. Congo Belge, III; Arthropodes, III; Crustacés, I, Fasc. 1.
- FAXON, W. 1893. 'Report of dredging operations off the west coast of Central America, . . . during 1891. VI. Preliminary descriptions of new species of Crustacea.' Bull. Mus. Comp. Zool., XXIV, Art. 7.
1895. 'Report of explorations off the west cost of Mexico, Central and South America and the Galapagos, . . . XV. The stalk-eyed Crustacea.' Mem. Mus. Comp. Zool., XVIII.
- GATES, W. H. 1910. 'Fifth biennial report of the Director. Gulf Biologic Station at Cameron, La.' Baton Rouge.
- GURNEY, R. 1924. 'Crustacea. Part IX. Decapod larvae.' British Antarctic ('Terra Nova') Exped. 1910, Nat. Hist. Rept., Zool., VIII, No. 2.
1927. 'Report on the larvae of the Crustacea Decapoda. Cambridge Exped. Suez Canal.' Trans. Zool. Soc. London, XXII, part 2, No. 15.
- HANSEN, H. J. 1919. 'Sergestidae of the Siboga Expedition.' Siboga-Expeditie XXXVIII. Leyden.
1922. 'Crustacés decapodes (Sergestides) provenant des campagnes des yachts "Hirondelle" et "Princesse Alice" (1885-1915).' Res. Camp. Sci. Monaco, LXIV.
1933. 'A North American species of *Acetes*.' Jour. Washington Acad. Sci., XXIII, Art. 1.
- HAY, W. P., AND SHORE, C. A. 1918. 'The decapod crustaceans of Beaufort, N. C.' Bull. U. S. Bur. Fisheries, XXXV (1915-1916). (Doc. No. 859).
- HELDT, H. 1931. 'Observations sur la ponte, la fécondation et les premiers stades du développement de l'oeuf chez *Penaeus carinatus* Risso.' C. R. Acad. Sci. Paris, CLXIII.
1932. 'Sur la fécondation chez . . . *Parapenaeus longirostris* Lucas.' C. R. Acad. Sci. Paris, CLXLIV.
- HELLER, C. 1862. 'Beitrag zur Crustaceen Fauna des Rothen Meeres.' Sitzungsber. k. Akad. Wiss. Wien, Math. Naturw. Cl., XLIV, Abt. 1.
- HOLMES, S. J. 1895. 'Notes on West American Crustacea.' Proc. California Acad. Sci., (2) IV.
1900. 'Synopsis of California stalk-eyed Crustacea.' Occasional Papers California Acad. Sci., VII.

- IVES, J. E. 1891. 'Crustacea from the northern coast of Yucatan, the harbor of Vera Cruz, . . . ' Proc. Acad. Nat. Sci. Philadelphia, XLIII.
- JOHNSON, J. Y. 1863. 'A new species of *Penaeus* from Portugal.' Proc. Zool. Soc. London.
- KEMP, S. W. 1909. 'Decapods of the genus *Gennadas*.' Proc. Zool. Soc. London.
1910. 'Macrura from the west coast of Ireland.' Fisheries, Ireland Sci. Invest., Dublin, I.
1917. 'Notes on Crustacea Decapoda in the Indian Museum. VIII. The genus *Acetes*.' Rec. Indian Mus., Calcutta, XIII, part 2, No. 7.
- KINGSLEY, J. S. 1878. 'Notes on North American Caridea in the museum of the Peabody Academy of Science.' Proc. Acad. Nat. Sci. Philadelphia, XXX.
1879. 'On a collection of Crustacea from Virginia, North Carolina, and Florida.' Proc. Acad. Nat. Sci. Philadelphia, XXXI.
- KISHINOUE, K. 1900. 'Japanese species of the genus *Peneus*.' Jour. Fisheries Bur., VIII, Art. 1, Tokyo.
1905. 'On a species of *Acetes* from Japan.' Annot. Zool. Japonensis, V, Art. 4.
- KOELBEL, C. 1884. 'Carcinologisches.' Sitzungsber. k. Akad. Wiss. Wien, Math. Naturw. Cl., XC, Abt. 1.
- LATREILLE, P. A. 1817. 'Nouveau Dictionnaire d'Histoire Naturelle,' XXV. Paris.
- LENZ, H., AND STRUNCK, K. 1914. 'Die Dekapoden der Deutsche Südpolar Expedition. I. Brachyuren und Macruren.' Deutsche Südpolar Exped. 1901-1903, XV. Zoologie VII, Heft 3. Berlin.
- LINNAEUS, C. 1767. 'Systema Naturae.' 12th Ed., Holmiae.
- LUCAS, H. 1849. 'Exploration scientifique de l'Algerie.' Zoologie. I. Animaux Articulés, part 1. Paris.
- MIERS, E. J. 1878. 'Notes on the Peneidae in the collection of the British Museum.' Proc. Zool. Soc. London.
1884. 'Report on the zoological collections of H. M. S. "Alert." Crustacea.' London.
- MILNE-EDWARDS, A., AND BOUVIER, E. L. 1909. 'Report on the results of dredging in the Gulf of Mexico, . . . by the U. S. Coast Survey Steamer "Blake." XLIV. Pénéides et Sténopides.' Mem. Mus. Comp. Zool., XXVII, Art. 3.
- MILNE-EDWARDS, H. 1830. 'Description des genres de l'Ordre des Crustacés Décapodes.' Ann. Sci. Natur., XIX.
1837. 'Histoire Naturelle des Crustacés.' II. Paris.
- MOUCHET, S. 1932. 'Sur l'appareil génital mâle de *P. trisulcatus* Leach.' Bull. Soc. Zool. France, XLVI (5).
- ORTMANN, A. E. 1890. 'Die Dekapoden-Krebse der Strassburger Museums, I.' Zool. Jahrb., Abt. für Syst., V.
1893. 'Dekapoden und Schizopoden der Plankton-Expedition.' Kiel und Leipzig.
1901. 'Crustacea, Zweite Hälfte: Malacostraca.' In Bronn, 'Klassen u. Ordnungen des Tier-Reich,' V, Abt. 2. Leipzig.

- RATHBUN, M. J. 1897. 'List of the decapod Crustacea of Jamaica.' Ann. Inst. Jamaica, I.
1901. 'Brachyura and Macrura of Porto Rico.' Bull. U. S. Fish Comm., XX (1900), part 2.
1902. 'Papers from the Hopkins Stanford Galapagos Exped. 1898-1899. VIII, Brachyura and Macrura.' Proc. Washington Acad. Sci., IV.
1904. 'Decapod crustaceans of the northwest coast of North America.' Harriman Alaska Exped., X, New York.
1906. 'Brachyura and Macrura of the Hawaiian Islands.' Bull. U. S. Fish Comm., XXIII (1903).
- SAY, T. 1818. 'An Account of the Crustacea of the United States.' Jour. Acad. Nat. Sci. Philadelphia, I, Art. 2.
- SCHMITT, W. L. 1921. 'Marine decapod Crustacea of California.' Univ. California Publ. Zool., XXIII.
1924. 'Expedition of the California Academy of Sciences to the Gulf of California in 1921. Crustacea (Macrura and Anomura).' Proc. California Acad. Sci., (4) XIII (1923).
- 1926a. 'Report on Crustacea Macrura (Peneidae, Campylonidae, Pandalidae) obtained by the F. I. S. "Endeavor" in Australian Seas.' Biological Results of the Fishing Experiments, V, Art. 6, Sydney.
- 1926b. 'Crustaceans collected by the American Museum Congo Expedition.' Bull. Amer. Mus. Nat. Hist., LIII.
1931. 'Two new species of shrimp from the Straits of Formosa.' Lingnan Sci. Jour. Canton, X.
- SEBA, ALBERTUS. 1758. 'Thesauri.' III. Amstelaedami.
- SENNA, A. 1903. 'Esplorazione abissali nel Mediterraneo.' II. Nota sui Crostacei Decapodi. Bull. Soc. Ent. Ital., XXIV.
- SMITH, S. I. 1871. 'Notice of the Crustacea collected by Prof. C. F. Hartt on the coast of Brazil.' Trans. Connecticut Acad. Arts Sci., II (1869).
1881. 'Preliminary notice of Crustacea dredged off the coast of New England.' Proc. U. S. National Museum, III.
1886. 'On some genera and species of Penaeidae.' Proc. U. S. National Museum, VIII (1885).
1887. 'Report on the decapod Crustacea of the "Albatross" dredgings off the east coast of the United States during the summer and autumn of 1884.' Rept. Comm. Fish and Fisheries for 1885, part 13, Appendix 2, Art. 21. Washington.
- SPAULDING, H. M. 1908. 'Life history and habits of the lake shrimp (*Peneus setiferus*).' Bull. Gulf Biologic Station, XI, Baton Rouge.
- STEBBING, T. R. R. 1914. 'South African Crustacea. Part VII.' Ann. South African Museum, XV.
1915. 'South African Crustacea. Part VIII.' Ann. South African Museum, XV.
- 1917a. 'South African Crustacea. Part IX.' Ann. South African Museum, XVII.
- 1917b. 'The Malacostraca of Durban Bay.' Ann. Durban Museum, I, part 5, Art. 22.

- STIMPSON, W. 1871. 'Notes on North American Crustacea in the Museum of the Smithsonian Institution, No. III.' Ann. Lyceum Nat. Hist., New York, X (1874).
- STREETS, T. H. 1871. 'Catalogue of Crustacea from the Isthmus of Panama.' Proc. Acad. Nat. Sci. Philadelphia, XXIII (1872).
- VERRILL, A. E. 1922. 'Decapod Crustacea of Bermuda. II. *Macrura*.' Trans. Connecticut Acad. Arts Sci., XXVI.
- VIOSCA, P. P., JR. 1920. 'Report of the biologist.' Fourth Biennial Report, Department of Conservation of Louisiana. Baton Rouge.
1923. In Tulian, 'The present status of the Louisiana shrimp industry.' Trans. American Fisheries Soc., LIII.
- WEYMOUTH, F. W., LINDNER, M. J., AND ANDERSON, W. W. 1932. 'A summary of the life history of the common shrimp (*Penaeus setiferus*).' Trans. American Fisheries Soc., LXII.
- WOOD-MASON, J., AND ALCOCK, A. 1891. 'Natural history notes from H. M. Survey Ship "Investigator," II.' Ann. Mag. Nat. Hist., (6) VIII.









